Environmental & genetic variation in blackwood (*Acacia melanoxylon* R.Br.) survival, growth, form & wood properties

by

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Statement of originality

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Where the candidate has co-authored a manuscript submitted for publication, the candidate undertook the research and major writing presented in this thesis. Co-authors oversaw the research project, and assisted with data analysis and text preparation in a supervisory role.

Gordon J Bradbury

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Abstract

Australian blackwood (*Acacia melanoxylon* R.Br.) is a high-quality appearance-grade timber species native to eastern Australia and renowned for its rich heartwood colour. It is grown in plantations in Australia and other countries but with mixed results. This is due in part to variable survival, growth, stem form and wood properties, including heartwood colour. The aim of this project was to determine the potential for genetic improvement of these traits by examining their environmental and genetic control. A review of available genetic resources showed that extensive native population provenance and family seed collections have been made with over 60 progeny trials established in both Australia and overseas. However, there are few published papers, particularly on wood properties.

Six family/provenance trials were identified as suitable for use in this project. These mainly contained open-pollinated families from Tasmania. Significant environmental (i.e. trial) and genetic variation in survival, growth, and form were found, with greater genetic variation between families within seed zones than between seed zones. Several mainland provenances were included in some trials and showed that blackwood from tropical Queensland was poorly adapted to survive in cool temperate Tasmania. Narrow-sense heritabilities for early age growth and form were significant, but moderate to low respectively. There were no significant genetic correlations between growth and form traits.

Wood properties were measured using stem cores on a sub-sample of 16 Tasmanian families across three 19 year-old trials growing at two sites. One site contained two spatially intermixed trials, with and without a *Eucalyptus globulus* nurse crop. Significant genetic, environmental and genetic by environmental interactions were

found for most wood properties, including heartwood colour. The presence of a nurse crop improved tree form but had an adverse effect on growth and wood colour. Stem diameter was not significantly genetically correlated with any of the wood properties, suggesting that selection for improved growth should not compromise wood properties. While environmental factors clearly affect growth and wood properties, the detection of significant genetic variation in most traits studied indicate that there is clearly potential for genetic improvement of growth, form and wood properties in blackwood.

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Format of thesis chapters

Chapters 3 to 7 of this thesis have been written in the format of scientific journal articles. Chapters 4 and 5 had been published at the time of thesis submission. Chapter 5 has a combined Results and Discussion section in line with the preferred format of the publishing journal. Chapter 2 was presented and published as a conference paper. Acknowledgements and references have been combined into single combined lists for the whole document. Introductions and conclusions are presented in each experimental chapter, with a general discussion highlighting key findings, implications and opportunities for continuing research.

Publications and other output from this project

Peer reviewed publications

Bradbury GJ, Beadle CL, Potts BM (2010) Genetic control in the survival, growth and form of *Acacia melanoxylon*. *New Forests* 39: 139 – 156 (Chapter 4)

Bradbury GJ, Potts BM, Beadle CL (2010) Phenotypic variation in wood colour in *Acacia melanoxylon* R.Br. *Forestry* 83: 153 - 162. (Chapter 5)

Conference papers & posters

Bradbury GJ, Beadle CL (2007) Genetic resources in blackwood: a mini-review. In 'Acacia Utilisation and Management: Adding Value – Proceedings of the 3rd Blackwood Industry Group (BIG) workshop'. (Eds CL Beadle and AG Brown) pp. 101-107. (RIRDC Publication No. 07/095, Canberra, Australia: 26-29 April 2006, Marysville, Victoria) (Chapter 2)

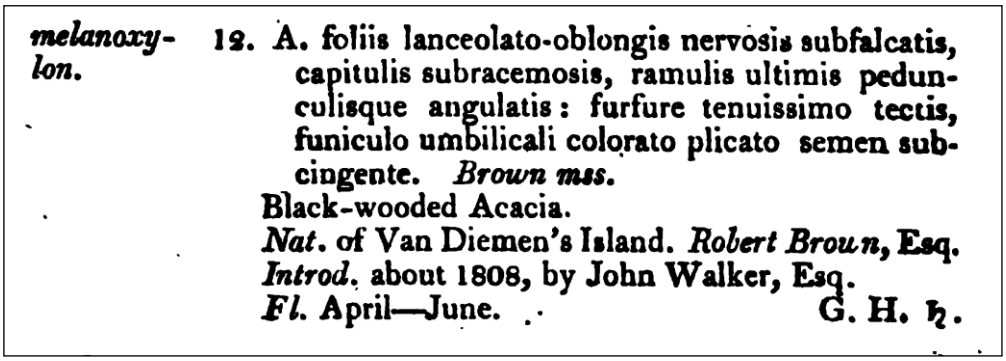
Bradbury GJ, Beadle CL, Potts BM (2007) Variation in growth and form in Tasmanian Blackwood. Poster presented at the 1st *Australasian Forest Genetics Conference*, 11 - 14 April 2007 Hobart, Tasmania.

Bradbury GJ, Beadle, C, Potts, BM (2009). Phenotypic and genetic variation in wood colour in Australian Blackwood (*Acacia melanoxylon* RBr.). Paper in 'Proceedings of 2nd *Australasian Forest Genetics Conference*, 20 - 22 April 2009, Freemantle, Western Australia. (CD ROM)

Preface

My interest in blackwood comes as much from a cultural and historical context as a scientific curiosity. Blackwood represents a cultural icon amongst Australian timbers whose origins go back to the earliest days of European settlement. Robert Brown, the English botanist assigned to the *Investigator* captained by Matthew Flinders, provided the first scientific description of blackwood. Brown spent three and a half years in Australia, collecting and recording botanical specimens, including becoming personally involved in the initial European settlement of Tasmania, accompanying Lieutenant Governor David Collins in establishing Hobart in February 1804. The original description of *Acacia melanoxylon* by Robert Brown (Figure i), from *Hortus Kewensis* p. 462 (Aiton 1813), is based on collections made by Brown on the Tamar and Derwent Rivers, Tasmania between 1803 and 1804 (Mabberley 1985; Maslin and Cowan 1995; Vallance *et al.* 2001).

Figure i: Original description of *Acacia melanoxylon* by Robert Brown in Aiton (1813).



melanoxylon. 12. A. foliis lanceolato-oblongis nervosis subfalcatis, capitulis subracemosis, ramulis ultimis pedunculisque angulatis: furfure tenuissimo tectis, funiculo umbilicali colorato plicato semen subcingente. *Brown mss.*
Black-wooded Acacia.
Nat. of Van Diemen's Island. *Robert Brown*, Esq.
Introd. about 1808, by John Walker, Esq.
Fl. April—June. G. H. ħ.

Blackwood timber was in use at least from 1803. A tea caddy (Figure ii) that belonged to Lieutenant Governor David Collins, made in part from blackwood (*c.* 1803), was auctioned in Melbourne in 2007 (Bonham & Goodman 2007; Davies 2008).

Figure ii: Tea caddy made from a variety of timbers including blackwood c 1803.

Blackwood sawmilling in Tasmania commenced in the 1830's, with production increasing in the 1880's with the widespread introduction of steam-powered sawmills, and the opening up of the blackwood-rich forests of Circular Head (Pink and Ebdon 1988; Brown 2001). About the same time blackwood production in Victoria increased as blackwood-rich areas of Gippsland were opened up for settlement (Featherston 2007). Since then blackwood has established a reputation as a fine furniture, joinery, tonewood and craft timber. Because of its wide ecological range and rapid growth it has the potential to remain an Australian timber "icon" through plantation development. However due to various silvicultural issues, and wide variation in important wood properties such as basic density and heartwood colour, it has not been an easy species to domesticate. While considerable research has been done on blackwood silviculture, there has been little research on blackwood genetics and wood properties. This project focused on existing early- and mid-age progeny trials in Tasmania to gain a better understanding of both the genetic and environmental effects on survival, growth, form and wood properties in blackwood.

Chapter 1: Introduction

Background

Description & Ecology

Australian blackwood (*Acacia melanoxylon* R.Br) is a small to large tree (6 – 45 m) widespread in eastern Australia, extending from the Atherton Tablelands in far-north Queensland (16°S) through the highlands of eastern Australia to Tasmania (43°S) and west into South Australia. It grows in a variety of habitats with best development in areas with fertile soils and high rainfall (Cowan and Maslin 2001). It is one of the most wide ranging tree species in eastern Australia with wide phenotypic variation (Farrell and Ashton 1978), and allozyme variation (Playford *et al.* 1993), both within and between populations.

Blackwood is prized for its wood and has a long history in Australia as a fine cabinet timber (Brown 2001). More recently it has attracted domestic and international interest as a tonewood in stringed musical instruments (Morrow 2007). The wood is characterised by dark-coloured heartwood with pale cream-coloured sapwood. However there is a wide variation in important wood properties including heartwood colour and basic density. This leads to problems in processing and production, and makes domestication as a plantation species difficult.

Domestication

Blackwood has been planted as an exotic in many countries, sometimes becoming an invasive weed (Nicholas 2007b). Current interest in blackwood as a plantation species is focused on New Zealand, China and Chile (Nicholas and Brown 2002; Zhang *et al.*

2004; Carranza 2007). China in particular has made much progress with the domestication of blackwood through multiple progeny trials, clonal and seedling seed orchards, and plantation development (Searle 2001). Chile has a small breeding program and a small but expanding plantation resource (Pinilla and Briones 2007). However, available genetic resources for selection and breeding remain limited, while the wide ecological range, and variation in growth, form and key wood properties, has slowed the domestication of blackwood. Matching superior genetic material with good sites, which result in good growth, form and wood properties, has so far proven difficult. Plantation-grown blackwood continues to generate domestic and international interest, with its established reputation as a quality timber, the potential for high growth rates, and wide ecological range.

Usage & Markets

Blackwood has a long established history in Australia as a premium appearance-grade timber being used in veneer, furniture, joinery, flooring, tonewood and craft (Brown 2001). Currently, the largest established market is in Australia, with smaller markets in South Africa and New Zealand. Australian markets are based on blackwood harvested from native forests, with most production coming from Tasmania (Featherston 2007; Forestry Tasmania 2008). South African markets are based on a small plantation resource and selective harvesting of former native-forest enrichment plantings and wildings (Geldenhuys 2004). Available timber volumes are limited, although production in New Zealand is expected to increase steadily from 2015 once existing plantations reach commercial maturity (Nicholas and Brown 2002).

Research

Research into blackwood began in the mid-1970's with Harrison's work on plantations in South Africa (Harrison 1974), and work by Mesibov in the swamps of north-west Tasmania (Forestry Tasmania 2005). The last ten years especially has seen a large volume of research published, including reviews from Australia (Searle 2000; Beadle *et al.* 2004), New Zealand (Nicholas and Brown 2002), Portugal (Santos *et al.* 2007), Chile (INFOR-CONAF 1998) and Argentina (Carranza 2007).

Survival, growth and form

Blackwood characteristics of variable growth rate, poor apical dominance and consequently poor stem form, susceptibility to browsing by mammals, and a degree of site sensitivity have slowed the pace of domestication of the species (Beadle *et al.* 2004). Nicholas and Brown (2002) list the essential site requirements for growing commercial blackwood as:

1. Shelter

   Shelter from strong and drying winds is critical, and is the main factor associated with good form. Shelter can be provided by topography, adjacent vegetation, or shelterbelt plantings.

2. Moisture

   Adequate moisture throughout the growing season is important for blackwood growth. Well-established trees can withstand occasional dry seasons and some drought, although commercial blackwood is not suited to drier sites.

3. Soil type

Blackwood grows best in mesic soils i.e. neither wet nor dry, that have reasonable fertility and a structure which retains moisture while allowing free drainage, but can also tolerate peaty or clay soils. On dry exposed sites, blackwood is slow growing, bushy, and prone to insect, particularly psyllid damage. Blackwood will tolerate occasional flooding, but will not grow in stagnant swamps.

4. Freedom from frost

Areas prone to severe frosts should be avoided. In New Zealand blackwood can suffer from severe out-of season frosts. Northern tropical provenances appear to be more susceptible to frost

Published diameter growth rates for blackwood in trials and plantations range between 0.2 and 4.3 cm yr^{-1}, with rates of >2.0 cm yr^{-1} not uncommon (Ryan and Bell 1991; Zhang *et al.* 1998). Height growth rates range from 0.3 to 4.0 m yr^{-1} with rates of 0.6–1.0 m yr^{-1} being commonly recorded. Growth models based on New Zealand plantation data for an average site index of 24 m (mean top height at base age 30 years) predict 290 m^3 ha^{-1} total standing volume at age 35 years at an annual MAI of 8.3 m^3 ha^{-1} and a mean diameter of 49 cm (Berrill *et al.* 2007). High quality sites are expected to produce around 400 m^3 ha^{-1} total standing volume at age 35 years. Diameter growth rates in native stands in Tasmania are modest in contrast to New Zealand plantation growth and range between 0.55 to 0.75 cm yr^{-1} in blackwood swamps (Forestry Tasmania 2005), and average 0.8 cm yr^{-1} as an understorey in eucalypt forest (Jennings 2007). So while good growth rates have been achieved in cultivation, and growth

models predict reasonable wood volumes on rotations of approximately 35 years, results have been variable.

Achieving good stem form is a major issue in growing commercial blackwood. Good stem form includes maintaining apical dominance and controlling branching. Apical dominance in blackwood has been found to be very much a function of the local light environment that is determined by the surrounding vegetation (Jennings *et al.* 2003; Medhurst *et al.* 2003; Pinkard 2003; Unwin *et al.* 2006), with insect predation also implicated (Appleton *et al.* 1997). Poor apical dominance has meant that intensive pruning is required in blackwood plantations to ensure the development of a single, straight, branch-free stem. While Nicholas and Brown (2002) list shelter as critical in improving stem form there is little published data to help define the parameters of shelter.

Previous research has taken little account of the wide geographical and ecological range of blackwood (Farrell and Ashton 1978). While previous studies have identified significant environmental and genetic variation in blackwood growth and form (de Zwaan and van der Sijde 1990; Neilsen and Brown 1996; Searle *et al.* 1998; Thinh *et al.* 1998; Zhang *et al.* 1998; Searle 2001; Zhang *et al.* 2004), most studies have used limited numbers of seedlots replicated across too few sites to assess the extent of genetic and environmental variation, or allow genetic material of superior growth and form to be identified.

Blackwood is very widespread within Tasmania from near sea level to 1000 m altitude, and from dry to very wet sites on a range of soils, so that significant variation in growth and form may be expected. The focus of the current study provides a major regional assessment of blackwood variation within a broad sample of Tasmanian genetic

material. In general more research is needed on environmental factors effecting blackwood growth and form. However improved growth and form is not by itself a sufficient basis for genetic selection due to the importance of wood properties, so that trials need to be maintained to a tree age/size that allows the assessment of heartwood properties.

Wood properties

Blackwood has many wood properties that are positive for an appearance-grade timber, including low growth stresses, ease of drying, low shrinkage, ease of dressing and sanding, in-service stability, ability to bend to shape, ability to take a high polish, and a dramatic heartwood colour range (Bootle 2005). Feature grain in blackwood is in high demaind with fiddleback, birdseye and raindrop being three recognised grain types. From a grower's and sawmiller's perspective, log diameter, heartwood colour and percentage heartwood are the most important traits (de Zwaan 1982). However markets are relatively unsophisticated both in Australia and overseas, with no account taken of the variation in other wood properties such as basic density. Nor is there much in the way of wood preference data for the various market sectors, with the few surveys identifying only broad market sectors and some general issues (Lambert 2004; Nicholas 2007d). With such a wide geographic and ecological range it may be expected that blackwood would show genetic variation in wood properties. However to date little research has been done to explore this variation.

Heartwood colour

Heartwood colour is a key wood property in blackwood. In comparison to other wood properties (e.g. strength, fibre length, lignin/cellulose content, etc.) the study of wood colour has received relatively little attention. Introductions and reviews of wood colour

research using colorimetry have been provided by Sullivan (1967b) and Vetter *et al.* (1990). Colorimetry has been applied to a variety of problems in wood science, such as changes in wood colour with different harvesting and processing techniques (Smith and Montoney 2000; Charrier *et al.* 2002; Mononen *et al.* 2002; Sundqvist 2002; Basri *et al.* 2003; Yeo and Smith 2003; Rappold and Smith 2004); and the study of wood colour differences between species (Sullivan 1967a; Nelson *et al.* 1969; Minemura *et al.* 1998; Nishino *et al.* 1998). Studies in phenotypic variation in wood colour within species from native forest (Klumpers *et al.* 1993; Burtin *et al.* 1998; Amusant *et al.* 2004; Bradbury 2005; Liu *et al.* 2005) and planted material (Rink 1987; Mosedale *et al.* 1996; Raymond and Bradley 2002; Hannrup *et al.* 2004; Thulasidas *et al.* 2006; Bhat *et al.* 2007; Grekin 2007; Moya and Berrocal 2010) have begun to define the wood colour range of individual species. However there have been few studies of the genetic and environmental variation and control of wood colour within a tree species.

The studies of Sotelo Montes *et al.* (2008) and Vanclay *et al.* (2008) represent the first attempts to quantify within-species genetic and environmental variation in wood colour, using extensive progeny material of *Calycophyllum spruceanum* in Peru and *Eucalyptus dunnii* in Australia respectively. Blackwood is known to occasionally show high within-tree heartwood colour variation, with tension wood being a known cause (Hillis *et al.* 2004). Therefore any study of variation in blackwood heartwood colour must include both between- and within-tree variation. Few studies have examined both between- and within-tree colour variation (Raymond and Bradley 2002; Sotelo Montes *et al.* 2008), with the development of practical sampling and measurement procedures still outstanding.

The accurate and repeatable measurement of colour requires understanding and controlling three elements: a) the object to be measured, b) the light source and c) the observer standard. The International Commission on Illumination (CIE) has set colorimetric standards for the correct measurement of colour using a range of light-source (illuminant) and observer standards (Wyszecki and Stiles 1982). The measurements can then be expressed in a range of colour scales or spaces. While there are several colour spaces that have historically been used in wood colorimetry (Sullivan 1967a; Nelson *et al.* 1969; Rink 1987; Wilkins and Stamp 1990), the colour space currently most commonly used is the CIELAB (Nishino *et al.* 1998; Janin *et al.* 2001; Raymond and Bradley 2002; Hannrup *et al.* 2004; Liu *et al.* 2005; Kokutse *et al.* 2006; Grekin 2007; Nicholas *et al.* 2007; Sotelo Montes *et al.* 2008; Vanclay *et al.* 2008). This colour space represents colour in three axes, the L* axis which records the lightness (0 black – 100 white), the a* axis which records the green (-ve) to red (+ve) values, and the b* axis which records the blue (-ve) to yellow (+ve) values.

The study of blackwood heartwood colour commenced with the work of Nelson and Heather (1970) who conducted a colorimetric assessment of wood colour across a wide range of Australian native timbers, including blackwood, albeit using a small number of samples per species. This was followed by the work of Harrison in South Africa (1974; 1975b; 1975a) who investigated heartwood content, and the genetic and environmental effects on heartwood colour and colour variation in blackwood plantations across South Africa. A visual colour grading system was used to assess heartwood colour and colour variation. A range of tree attributes were measured including tree age and size,and correlations tested against heartwood colour. Results from this work concluded i) heartwood content was proportional to the stem diameter-under-bark, ii) heartwood

content differed significantly between regions within South Africa, with the highest heartwood contents produced on moist, well-drained, deep, organic soils, iii) there was little apparent genetic variation between regions based on leaf morphological characteristics, such that any regional differences in wood properties may be assigned to environmental differences, iv) there was significant variation in colour with height in the tree, v) there were no significant between-tree weighted-mean heartwood colour difference within regions, but there were significant differences between regions as well as significant differences between regions in within-tree colour uniformity, vi) sites with a high number of rain days during the growing season, and a definite dormancy-producing season of cold, dry weather seem to be associated with darker, more uniform-coloured wood, and vii) heartwood colour was not significantly correlated with either tree age or tree size.

Blackwood heartwood colour research continued with Nicholas *et al.* (1994b) who analysed growth and wood properties from a small 10-year-old progeny trial in New Zealand. Both visual grading and colorimetry were used to assess heartwood colour. No significant difference in heartwood colour was detected between four seedlots, while significant differences were found in diameter growth rate, basic density, and green moisture content. Bradbury (2005) compared wood properties between two silvicultural treatments of Tasmanian native forest blackwood regrowth aged 14 to 22 years, with colorimetry used to measure heartwood colour. Significant differences in heartwood colour were found between treatments. Nicholas *et al.* (2007) compared wood properties across five sites in a silvicultural trial in New Zealand of 18 years of age, containing a single seedlot; including using colorimetry and visual grading to assess heartwood colour. Significant differences in colour were found between sites and between

silvicultural treatments. Lourenço *et al.* (2008) investigated the pulping properties of blackwood aged 28-to 43 years in Portugal, including the colour variation in heartwood and sapwood pulps. These studies demonstrated both environmental and genetic variation in heartwood colour in blackwood, but in relatively small trials.

Other wood properties

Non-colour wood properties of blackwood such as percentage heartwood, heartwood width, basic density, strength, hardness, shrinkage, and moisture content have been widely reported both for native forest, and Australian and overseas plantation material (Eckbo and Scott 1925; Greenhill and Dadswell 1940; Scott 1953; Kingston and Risdon 1961; Bolza and Kloot 1963; Sekhar and Kukreti 1979; Haslett 1986). However most data have been based on a limited number of samples, often of unknown age and origin. Differences in sampling and measuring methodology between sources may have contributed to the observed variation in reported results. Therefore the genetic and environmental variation in these non-colour wood properties, their intercorrelations, within-tree variation and variation with tree age remain poorly understood. What is apparent is that there is considerable variation in at least some of these properties, which has potential impacts on product quality and consistency, genetic selection, breeding and utilisation.

Significant environmental and genetic variation in some blackwood wood properties have been reported. Harrison (1974; 1975b) found that heartwood content was proportional to the stem diameter-under-bark and differed significantly between regions within South Africa, with the highest contents produced on moist, well-drained, deep, organic soils. Wilkins and Papassotiriou (1989) found significant differences in some wood anatomical features in native forest material of unknown age collected from

Queensland to Tasmania. However no significant difference in basic density was apparent between Queensland 521 (S.D.± 40) kg m^{-3} and Tasmanian 495 (S.D.±85) kg m^{-3} samples. Nicholas *et al.* (1994b) found significant differences in basic density and green moisture content between four seedlots. Bradbury (2005) found significant differences in wood properties between silvicultural treatments in native blackwood regrowth, while Searle and Owen (2005) found no significant difference in basic density or percentage heartwood between five blackwood provenances. Nicholas *et al.* (2007) found significant differences in wood properties between sites and silvicultural regimes.

Apart from radial wood colour variation the current study does not address within-tree variation in other wood properties. However within-tree studies are important for a) a general understanding of within-tree variation, b) an understanding of environmental and genetic variation and genetic control of within-tree variation, and c) for determining the best location for sampling mean tree values. A number of studies have examined within-tree variation in blackwood basic density (Haslett 1986; Ananías 1989; Searle and Owen 2005; Igartúa and Monteoliva 2009; Igartúa *et al.* 2009), heartwood colour (Harrison 1975a), heartwood content (Harrison 1974; Harrison 1975b; Knapic *et al.* 2006), and tension wood and cellular properties (Hillis *et al.* 2004) in blackwood. These studies have increased general understanding of within-tree variation in blackwood, but have not addressed objectives b) and c) above.

Three studies have examined intercorrelations between blackwood wood properties. Nicholas *et al.* (1994b) found significant genetic correlations between heartwood colour and percentage heartwood (-ve), green density and moisture content (+ve); percentage heartwood and green density (+ve) and moisture content (+ve); and green density and basic density (+ve) and moisture content (+ve). No phenotypic or genetic correlations

were found between diameter and either heartwood colour or basic density. Bradbury (2005) found significant strong negative phenotypic correlations between heartwood colour lightness and basic and green densities. Nicholas *et al.* (2007) found percentage heartwood was not significantly phenotypically correlated with diameter, while basic density was significantly and positively correlated with diameter.

These previous studies have indicated wide phenotypic and genetic variation in blackwood growth, form and wood properties. However, most studies have used a limited range of genetic material growing on very few sites. Until the current study little genetic research had been done into blackwood wood properties, including heartwood colour.

Objectives of this study

The objective of the current study was to utilize existing progeny trials in Tasmania to extend current knowledge of the environmental and genetic variation in survival, growth, form and wood properties in blackwood. A major focus of the study was to define the phenotypic, environmental and genetic variation in heartwood colour, and within- and between-tree heartwood colour variation.

Chapter 2: Genetic Resources in Blackwood

Introduction

There is a small but growing body of literature on blackwood provenance research. Interest in blackwood at this level comes as no great surprise, given the wide geographic range of the species and its adaptation to a range of environments. The disciplines of genetics and ecology are therefore likely to be very useful in improving the value of blackwood to production forestry. However, *A. melanoxylon* has a long history of use as a fine cabinet timber, this has always been into a small well-established market. This has meant that justification for and financial resources available in support of tree improvement programs have been limited and progress in this area of research very slow.

This short review focuses on available information on seed collections, provenance trials and published data from these trials. Much of the information from Tasmania can be found in Neilsen and Brown (1996), who summarised blackwood research up to that date. Information from other sources is more thinly spread and for some trials is non-existent. A broader summary of blackwood research that includes genetic resources can be found in Searle (2000), with updates from recent literature in the proceedings from the Blackwood Industry Group (BIG) workshops in 2000 and 2002 (eg. Stackpole 2001; Jackson *et al.* 2004; Pinilla *et al.* 2004; Zhang *et al.* 2004).

Seed collections

The available information on blackwood seed collections is mainly based on those collected in Tasmania and by the CSIRO Australian Tree Seed Centre (ATSC). For

many years the Forest Research Institute in New Zealand has had an interest in blackwood, and has maintained a blackwood seed collection.

As seed collections are the basic source of material for research into blackwood genetics, it is important to maintain accurate records of where the seed comes from, particularly its geographic location, and the number and distribution of parents.

Forestry Tasmania

Forestry Tasmania made extensive collections of blackwood seed between 1988 and 1993 when local interest in planting blackwood was high. Seed was collected from a total of 127 open pollinated families from native forest around Tasmania. In 1988 and 1989 seed was collected from single trees of superior phenotype. Seed collected between 1991 and 1993 was used to supplement previous collections from high-altitude populations and to provide additional trees so that comparisons between and within populations could be undertaken. These latter collections were made from random trees provided that seed trees were at least 100 m apart and each tree was not isolated or of poor form. Most trees were felled during seed collection. Some of the seedlots were from trees exhibiting fiddleback figure in the wood.

Of the 127 families collected, 108 contain at least 10 g of seed. This was deemed the minimum quantity necessary for future trial work. Neilsen and Brown (1996) arranged these 108 families into 22 groups based on location, climate, soils and altitude. Figure 2.1 shows the location of the 127 collection sites around Tasmania, together with the known distribution of blackwood in Tasmania (DPIW *online*). The 127 families represent a remarkably good sample from this distribution, with the possible exception of populations occuring in the south-east of the state and Flinders Island.

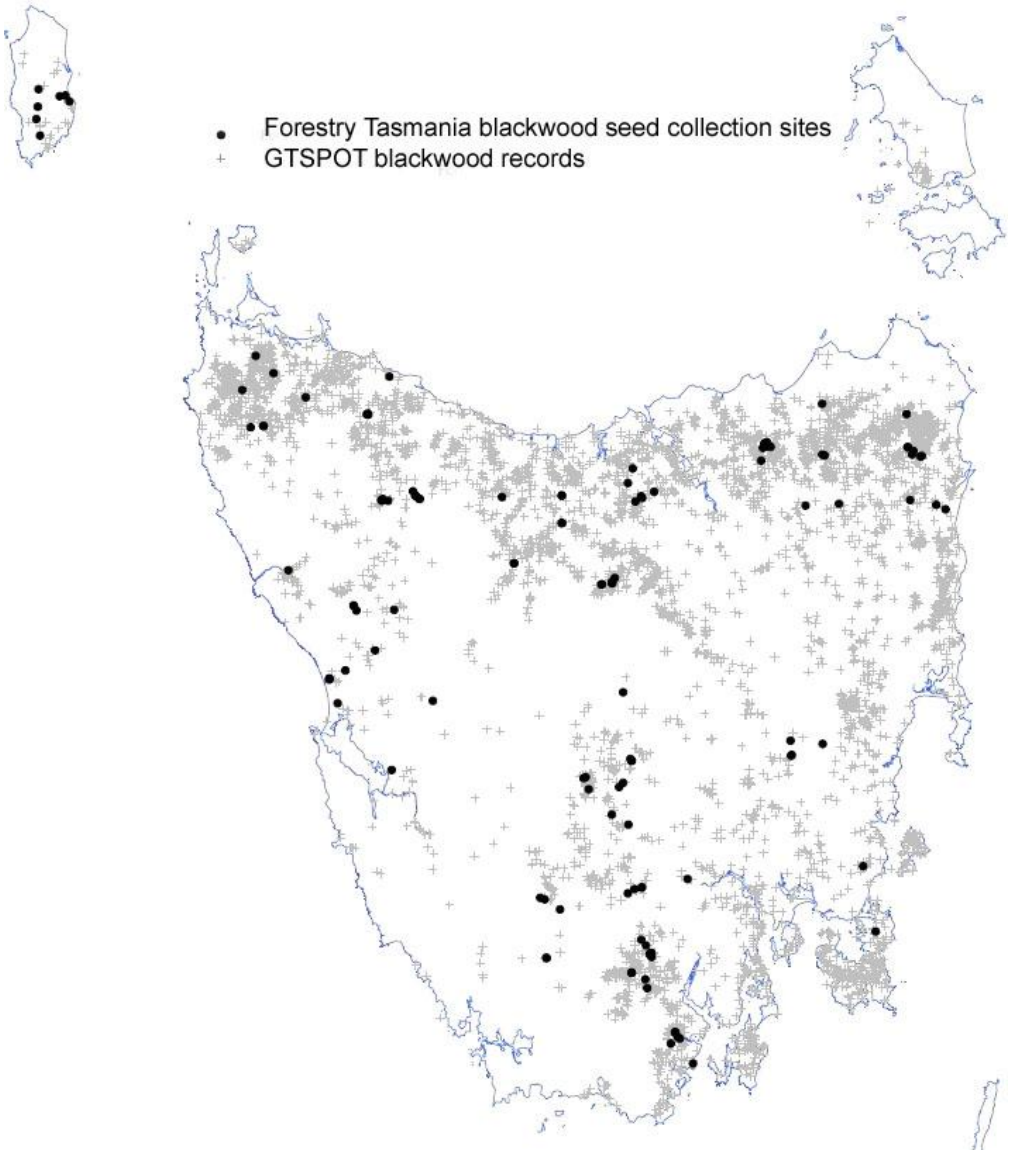


Figure 2.1: Forestry Tasmania blackwood research seed collection locations 1988 - 1991, overlaid with the Statewide distribution of the species from blackwood botancical records.

CSIRO Australian Tree Seed Centre

Since the 1970s CSIROs Australian Tree Seed Centre (ATSC) has had a significant tree seed collection program (Figure 2.2). During that time 89 provenance collections of blackwood are known to have been made with twenty-nine blackwood provenances composed of 347 families currently listed in the ATSC catalogue. These include

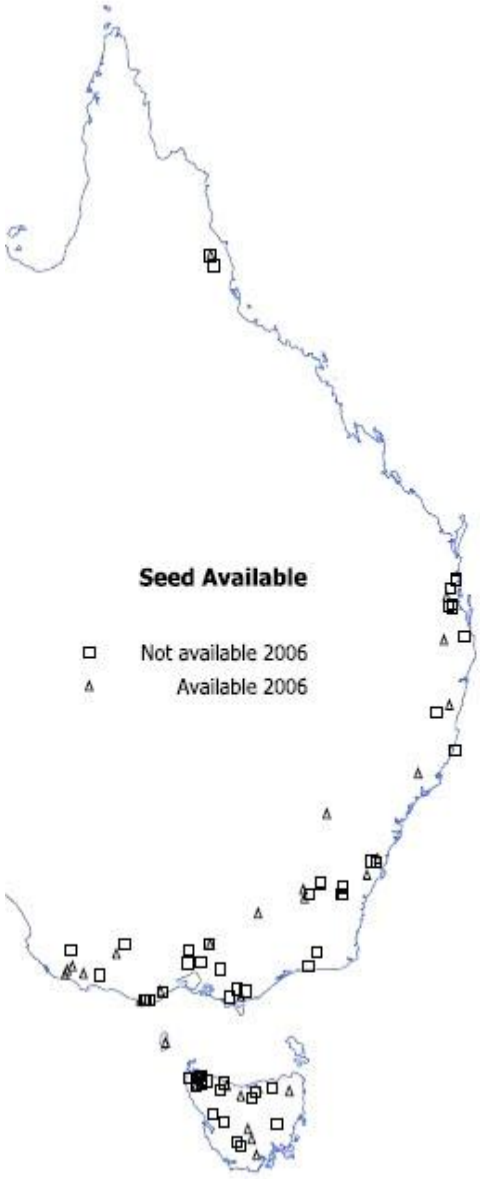


Figure 2.2: Location of past and currently (2007) available blackwood seed collection sites from the CSIRO Australian Seed Tree Centre.

examples from the full geographic range of the species from northern Queensland to southern Tasmania.

All seedlots must meet minimum standards for documentation. These standards are: seed collected from natural stands (unless specified), location of collection (including latitude, longitude and altitude), date of collection, number of trees in collection, minimum spacing of 100 m between trees and a minimum standard for seed cleanliness. For ATSC collections, additional documentation includes soil data, associated vegetation information, tree descriptions, phenological data, photographs and botanical specimens (Australian Tree Seed Centre online). A useful history of the ATSC is provided in FAO (2002).

New Zealand

New Zealand has had an interest in growing commercial blackwood since the late 19th century. This interest was given a new focus in 1981 when blackwood was included in the official New Zealand Forest Service Policy for Special Purpose Species (NZ Forest

Service 1981). Since that time blackwood has been adopted by an increasing number of New Zealand farmers who are taking up the market in growing and supplying premium-grade timbers. The Forest Research Institute of New Zealand (FRI) (formerly the New Zealand Forest Service) maintained a low-level blackwood research program, including a blackwood seed bank, until recently. This was made up of local sources and material from Tasmania, the ATSC, South Africa and Chile.

Provenance trials

Within the small body of published literature on blackwood provenance research, Tasmania and Victoria, New Zealand and China have been the major players.

Tasmania and Victoria

Fourteen blackwood provenance trials at seven sites have been established in Tasmania since 1988 (Table 2.1). Of these, ten are considered in more detail by Neilsen and Brown (1996). Of the four additional trials, two are at Westfield in the Florentine Valley, Tasmania, where one is a pure blackwood planting and another was established with a nurse crop. The third is a major trial established at Togari west of Smithton (114 families), Tasmania; and the fourth is a blackwood seed orchard at Oigles Road near Geeveston, Tasmania, which has the potential to provide the basis for valuable genetic research. These four trials have not been measured since establishment. Seven blackwood provenance trials were established in Victoria in 1993/1994 in the south-west and the north-east of the state. Early results from some of these trials have been published (Table 2.2).

ACT and Queensland

A major acacia species and provenance trial was established in the Australian Capital Territory (ACT) in 1994. The trial included five provenances of blackwood. Unfortunately one replicate of the trial (at Uriarra) was destroyed by wildfire in 2003. Applegate and Nicholson (1986) report the early results of two acacia species trials in Queensland that included two Queensland provenances of blackwood (Table 2.2).

Table 2.1: Blackwood provenance trials established in Tasmania.

Code	Location	Type	Nurse crop	Families	Replicates	Trees per plot	Total	Latitude	Longi-tude	Estab year
RP266/1/1	Meunna *	Block	*P. radiata*	20	2	80	3200	41.08	145.47	1988
RP226/1/2	Meunna *	Row	None	23	5	20	2300	41.08	145.47	1988
RP266/2/1	Meunna	Block	*P. radiata*	25	2	80	4000	41.08	145.47	1989
RP266/2/2	Meunna	Row	None	37	5	20	3700	41.08	145.47	1989
RP266/3/1	Smiths Plains	Block	*P. radiata*	7	2	26	364	41.43	146.00	1988
RP266/3/2	Smiths Plains	Row	None	9	5	20	900	41.43	146.00	1988
RP266/4/1	Virginstow	Block	*E. globulus*	15	2	80	2400	41.30	146.60	1988
RP266/4/2	Virginstow	Row	None	17	5	20	1700	41.30	146.60	1988
RP266/5/1	Round Hill	Row	*E. nitens*	39	3	15	1755	41.52	146.00	1993
RP266/6	Meunna	Row	*E. nitens*	48	2	10	960	41.08	145.47	1993
RP266/9/1	Westfield	Row	*A. dealbata*	24	1–6	20	630	42.65	146.43	1993
RP266/9/2	Westfield	Row	None	?	?	?	?	42.65	146.43	1993
RP266/10	Togari *	Row	*E. globulus*	114	5	5	2850	40.88	144.95	1997
	Oigles Rd	Row	None	114	6	3	2052	43.17	146.85	2000

Note: * Trial includes mainland provenances

New Zealand

Three blackwood provenance trials were established in New Zealand in 1960 (Table 2.2). The history of these quite small trials and results from their measurement have yet to be published, although Nicholas and Brown (2002) comment that their form was no better than that of trees from unselected sources. Subsequent trials, one established in 1983 and a major series of 15 trials established in 1984, represent a significant resource for genetic research (Table 2.2). The limited venture into blackwood clonal research in

New Zealand represents the first tentative step into the next phase of genetic research in blackwood.

China

Since the late 1980s China has developed a series of provenance trials that include blackwood (Table 2.2). A major blackwood trial containing 178 families was established in 1996 (Zhang *et al.* 2004).

Others

Three blackwood provenance trials containing 12 provenances were established in South Africa in 1976 and 1977 (Table 2.2). These are some of the oldest blackwood provenance trials (de Zwaan and van der Sijde 1990). Chile has recently commenced a blackwood improvement program. They have identified blackwood as having commercial potential in the small private grower market. Progeny trials containing 12 provenances were reported as being established (Pinilla *et al.* 2004).

Table 2.2: Known blackwood family (f)/provenance (p) trials outside Tasmania

State or country and location	Planted	Reference	Families/ prov	Rep	Trees per plot
Victoria					
Tallangatta	1993	(Stackpole 2001)	25p	5	6
Euroa	1993	(Stackpole 2001)	25p	6	6
Euroa	1993	(Stackpole 2001)	25p	9	6
Hensley Park	1993	(Jackson *et al.* 2004)	20p	2	10
Vasey	1993	(Jackson *et al.* 2004)	20p	2	10
Gringegalgona	1994	(Bird *et al.* 1996)	4p	4	10
Dunkeld	1994	(Bird *et al.* 1996)	4p	4	10
Bunyip	2003	(Chan and Lockwood 2007)	70f	8	3
Queensland					
Tuan	1985	(Applegate and Nicholson 1986)	2p	2	16
Kuranda	1985	(Applegate and Nicholson 1986)	2p	0	4
Australian Capital Territory					
Uriarra	1994	(Searle and Owen 2005)	5p	4	10
New Zealand					
Waitangi	1960	(NZ Forest Research Institute 1978)	10p		
Kaingaroa	1960	(NZ Forest Research Institute 1978)	10p		
Te Wera	1960	(NZ Forest Research Institute 1978)	10p		

State or country and location	Planted	Reference	Families/ prov	Rep	Trees per plot
Tauranga *(Hosking)*	1983	(Nicholas *et al.* 1994b)	4p		
Tairua NI	1984	(Stehbens 1992)	30p		
Whakarewarewa NI	1984	(Stehbens 1992)	30p		
Kaingaroa (I) NI	1984	(Stehbens 1992)	30p		
Kaingaroa (II) NI	1984	(Stehbens 1992)	30p		
Wairau (Blenheim) SI	1984	(Franklin 1987)	30p		
Longwood (Otautau) SI	1984	(Franklin 1987)	30p		
Golden Downs (Nelson) (I) SI	1984	(Stehbens 1992)	30p		
Golden Downs (Nelson) (II) SI	1984	(Stehbens 1992)	30p		
Reefton (I) SI	1984	(Franklin 1987)	30p		
Reefton (II) SI	1984	(Franklin 1987)	30p		
Mawhera (Greymouth) SI	1984	(Stehbens 1992)	30p		
Mahinapua (Hokitika) (I) SI	1984	(Stehbens 1992)	30p		
Mahinapua (Hokitika) (II) SI	1984	(Stehbens 1992)	30p		
Strathallan (Dipton) (I) SI	1984	(Stehbens 1992)	30p		
Strathallan (Dipton) (II) SI	1984	(Stehbens 1992)	30p		
Clonal plantings (*Gibson-Smith*)	1991	(Nicholas and Brown 2002)			
China					
Shangyong forest farm, Hainan Island	1987	(Zhang *et al.* 2004)	2p		
Zhuhai, Guangdong	1988	(Zhang *et al.* 2004)	3p		
Longtouxue forest farm, Guangdong	1989	(Zhang *et al.* 2004)	3p		
Longtouxue forest farm, Guangdong	1990	(Zhang *et al.* 2004)	4p		
Hekou forest farm, Guangdong; Ruijin County, Jiangxi	1991	(Zhang *et al.* 2004)	21p		
Timian Huadu, Guangdong; Longdong forest farm, Guangdong.	1992	(Zhang *et al.* 2004)	6p		
Shixing, Guangdong and Ganzhou, Jiangxi	1994	(Zhang *et al.* 2004)	5p		
Shixing, Guangdong	1995	(Zhang *et al.* 2004)	5p		
Conghua, Kaiping, Enping; Jiangmen Guangdong	1995	(Zhang *et al.* 2004)	4p		
Gudoushan, Longdong; Shunao forest farms Guangdong	1996	(Zhang *et al.* 2004)	35p 178f	8	3
Dongguan Guangdong	1997	(Zhang *et al.* 2004)	20f		
Luofeng Guangdong	1998	(Zhang *et al.* 2004)	2p		
Shantou Guangdong	1999	(Zhang *et al.* 2004)	2p		
Jiangmen Guangdong	2000	(Zhang *et al.* 2004)	35 clones		
South Africa					
Blueliliesbush	1976	(de Zwaan and van der Sijde 1990)	12p	6	49
Jonkersberg	1976	(de Zwaan and van der Sijde 1990)	12p	6	49
Spitskop	1977	(de Zwaan and van der Sijde 1990)	12p	4	36
Chile		(Pinilla *et al.* 2004)	12p		

NI = North Island, SI = South Island.

Published data

While Tables 2.1 and 2.2 show an impressive list of blackwood provenance research trials, the list of published results emerging from these resources has been disappointingly small.

Australia

The early (age 3 – 8 years) results from the ten provenance trials in Tasmania referred to in Neilsen and Brown (1996) indicate significant differences between provenances for height and survival for most trials. There were no substantial differences in growth and survival between Tasmanian, Victorian and southern New South Wales (NSW) provenances. For Tasmanian provenances, there was no consistent trend between the effect of groupings by provenance origin on the variables measured, except for frost: the high-altitude north-east and far north-west provenances were consistently more susceptible to frost than other provenances. Since this publication, many of these trials have not been managed as originally planned. Consequently there has been a reduction in their research value.

Stackpole (2001) published early (age 8 years) results for the Victorian trials at Euroa and Tallangatta. He found significant differences in both basal area growth and form between provenances at both sites. Some provenances were identified that exhibited superior growth and form, and therefore had potential for further investigation.

Jackson *et al.* (2004) published early (age 10 years) results for two blackwood trials in south-western Victoria. At both sites there were significant differences (p <0.05) in height, dbhob and form between the provenances tested. There was no significant interaction between provenance and nurse-crop treatments. Provenance rankings were

different between sites. There were some differences in provenance performance based on groupings by provenance origin based on altitude and rainfall.

Applegate and Nicholson (1986) reported results at age 12 months from acacia species trials in Kuranda and Tuan, Queensland. The blackwood provenance from Nambour, south-eastern Queensland, performed better at both sites than the provenance from Atherton, far-northern Queensland.

Searle and Owen (2005) reported results at age 8 years from a set of acacia species trials in the ACT that included blackwood provenances from Queensland, South Australia, Tasmania and Victoria. This analysis included wood basic density and percentage heartwood measurements. Whole-tree, volume-weighted mean basic densities were not significantly different between the five blackwood provenances tested. There were highly significant differences (p <0.001) in percentage heartwood among the provenances. One provenance from the Grampian Ranges, Victoria had no discernable heartwood (0%) but also had the highest mean basic density of the five provenances.

Other

Data at age 10 years from the Tauranga progeny trial in New Zealand are presented in Nicholas *et al.* (1994b). There were statistically-significant differences between four seedlots, two from South Africa and two from Tasmania, in dbhob, basic density and green moisture content. No significant differences between seedlots were observed in percentage heartwood and heartwood colour.

Franklin (1987) showed that there was wide variation in frost resistance of individuals within provenances across the 1984 trials in New Zealand at age 2 years (Table 2.2). It

was not uncommon to find seedlings killed by frost located quite close to others of the same origin showing little or no frost damage. No statistical analysis was undertaken. However, in general, Tasmanian seedlots were more frost hardy than other Australian, New Zealand, Chilean or South African seedlots, although the Tasmanian seedlots had below-average height growth on the sites assessed. Stehbens (1992) also reported early (age 8 years) results from four of the sites of this 1984 trial series. A complete later-age assessment of the New Zealand 1984 trial series remains a significant opportunity for the blackwood research community.

In 1988 the New Zealand Forest Research Institute identified 74 trees of good form from North Island plantations and collected root cuttings from them. Of the 35 clones that were successfully rooted, 26 were archived on two sites north of Auckland in 1991. Measurements at age 6 years showed considerable variation in stem form amongst individual clones within sites and none had the good form that was a feature of the mother trees (Nicholas and Brown 2002). The reason for this outcome remains unknown. Appleton *et al*. (1997) have suggested that blackwood form may be as much a function of insect attack as genetics and physical environment.

In the South African trials (Table 2.2), de Zwaan and van der Sijde (1990) found significant differences between provenances in dbhob up to age 10 years. Seedlots from Stawell in Victoria, Collingwood River in Tasmania and Tallaganda in NSW were the poorest performers in all trials. Identifying the best performers was more difficult. A later-age remeasurement of this series of trials would provide a very useful set of data, particularly if it included an analysis of wood properties.

In the large trial established in 1996 in Guangdong Province, China, measured at age 14 months, Zhang *et al.* (2004) showed that there was significant provenance and family

variation for survival, height and stem number. Variation for these traits was greatest within families, followed by that between families and then between provenances. Queensland and NSW provenances performed best at this tropical high-rainfall site. Results from the other provenance trials in China remain to be published.

Conclusion

This review indicates that the major focus in blackwood genetic research in the past 40 years has been in seed collection (over 200 collection sites) and trial establishment (over 60 trials). The few published results from these trials have generally been for trees aged 10 years or younger. Significant differences in growth between provenances and between families have been demonstrated. Surprisingly, only two studies have examined genetic differences in wood properties. This is despite the fact that variation in wood properties has been well documented.

There are considerable research opportunities to be realised from the experimental trials already established. An obvious example is the remeasurement of the more comprehensive Tasmanian, New Zealand and South African trials, including wood sampling and analysis. Given the continuing issues that surround growth and particularly form in blackwood, more detailed studies of factors affecting form such as insect predation would yield significant benefits.

Given the national and global spread of the tiny blackwood research community, a collaborative approach can only benefit all players. Links with other acacia research communities, for example those based on tropical acacias like *Acacia koa* will also be of benefit to the blackwood research community. Those jurisdictions that are reducing their interest in blackwood research but retain significant assets, for example South Africa,

should be encouraged to at least retain their assets until final measurement and sampling can be arranged.

Chapter 3: Genetic Variation in Early-Age Survival, Growth and Form of *Acacia melanoxylon*

Introduction

Australian blackwood (*Acacia melanoxylon* R.Br.) is a species that yields high quality, appearance-grade timber, and is one of the most wide-ranging tree species in eastern Australia (Cowan and Maslin 2001). It has considerable phenotypic (Farrell and Ashton 1978) and allozymic (Playford *et al.* 1993) variation. Interest in genetic improvement of the species is stimulated by its reputation for high quality wood and potentially high growth rates, but domestication is still at a very early stage.

There has been extensive blackwood silvicultural research in native forest (Jennings *et al.* 2003; Unwin *et al.* 2006; Jennings 2007; Unwin and Jennings 2007) and plantations (Nicholas and Brown 2002; Pinkard and Beadle 2002; Medhurst *et al.* 2003; Beadle *et al.* 2004) that has identified a range of important site selection and management issues. In contrast research into genetic variation within the species has been minor despite its wide ecological range and genetic diversity (Searle 2000). Most genetic studies have involved few seedlots and limited replication, however significant between- (de Zwaan and van der Sijde 1990; Nicholas *et al.* 1994b; Searle *et al.* 1998; Stackpole 2001; Zhang *et al.* 2004) and within-region (Jackson *et al.* 2004; Zhang *et al.* 2004) genetic differences in survival, growth and stem form have still been recorded.

Significant differences in survival, growth, and form between a selection of later-age Tasmanian families are discussed in Chapter 4, however the sample of families was too small to detect any geographic patterns in genetic variation. The present study is based

on a progeny trial in southern Tasmania testing 102 Tasmanian families. The objectives of the study were to 1) determine the extent of genetic variation in early-age blackwood survival, growth and stem form, and 2) determine the phenotypic and genetic correlations between these traits.

Materials and Methods

Trial

The trial assessed in this study was established in 2000 at Oigles Road near Geeveston in southern Tasmania, with the intention of developing a commercial seed orchard (Figure 3.1, Table 3.1). The trial tested 102 open-pollinated single-tree families of blackwood collected from around Tasmania between 1988 and 1993 (Appendix 1). Seed collected in 1988 and 1989 was from "single trees of superior phenotypic form, with attention being paid to high and low altitude seedlots in each of 12 seed zones" (Allen 1992). Seed collected in 1991 - 1993 was to supplement both high and low altitude material and was made from trees selected at "random" provided trees were at least 100 m apart, not isolated, and of at least reasonable form (Neilsen and Brown 1996). The 12 seed zones were defined in 1988 especially for blackwood provenance research in Tasmania, based on broad geographic, topographic and climatic classes (Forestry Commission Tasmania *unpublished*). The number of families per seed zone in the trial varied from 4 to 18.

The trial comprised six replicates, each containing four incomplete blocks. Each incomplete block contained 26 family plots with families arranged in 3-tree line plots. The initial trial design was generated using the software program CycDesigN (Williams *et al.* 2002). However, this was modified because of the variable number of seedlings

available for each family, arising from small numbers of seeds and poor germination in some families. Families that had extra seedlings were used to fill in positions of those that had insufficient seedlings. This resulted in 38% of families being represented more than once in a replicate, and 39% being omitted from one or more replicates. The trial was planted using a spacing of 2.0 m between trees and 3.1 m between rows for a stocking rate of 1612 stems per hectare. The trial had not received any thinning or pruning treatment at the time of measurement.

Table 3.1: Blackwood trial design and attributes.

Attribute	Value
Year planted	2000
Latitude (°S)	43°10’
Longitude (°E)	146°51’
Altitude (m)	260
Aspect	North West
Slope	0 - 20°
Mean annual rainfall (mm)	1000
Mean winter min and summer max temperatures	2.2 - 21.7°
Tasmanian families	102
Replicates	6
Blocks per replicate	4
Plots per block	26
Trees per plot	3
Stocking (stems.ha^{-1})	1612
Trial area (ha)	1.1

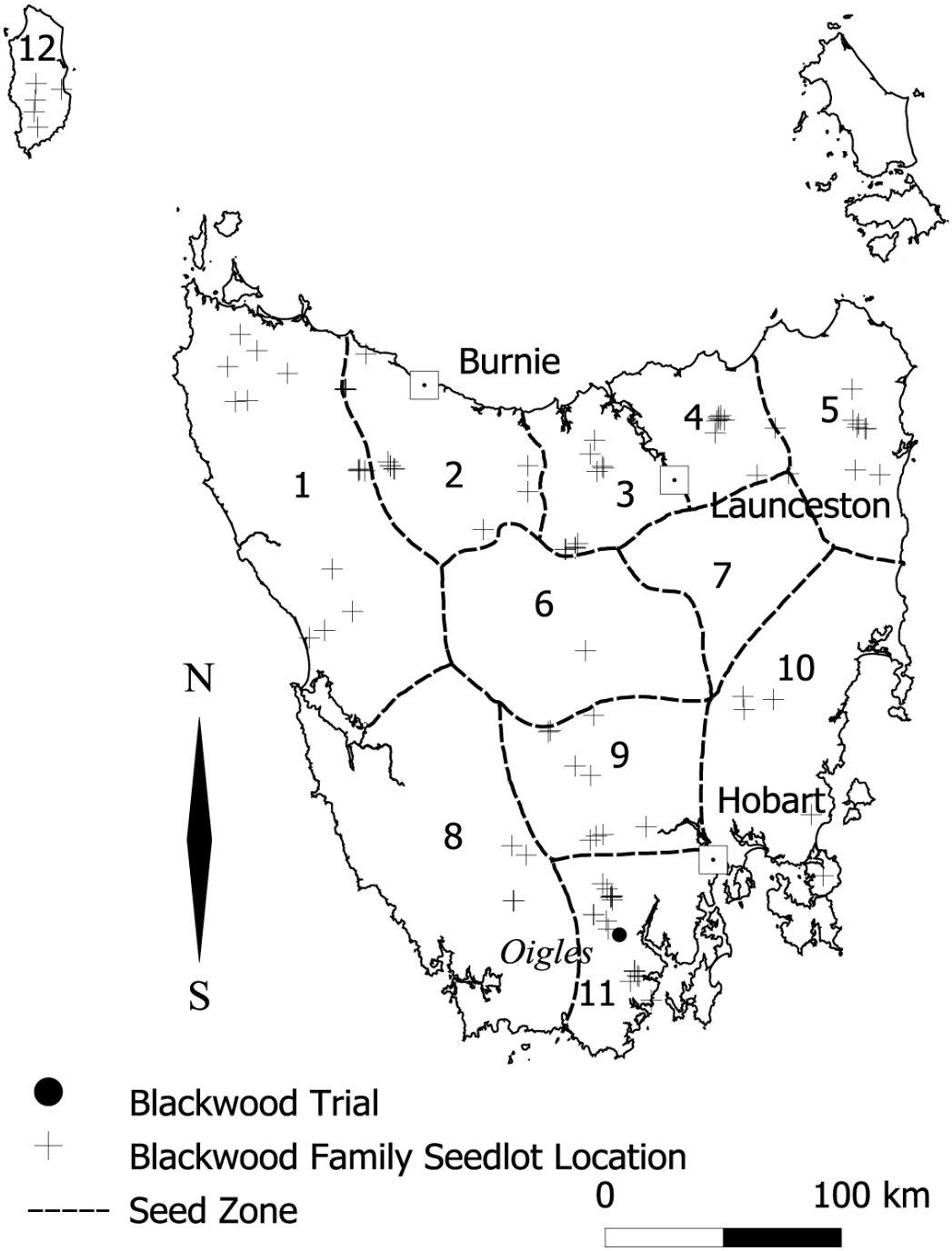


Figure 3.1: Tasmania showing the location of the Oigles Road trial, and the collection sites of the family seedlots and seed zones. The seed zones are 1 (Far north-west & west coast), 2 (North-west coast), 3 (West Tamar), 4 (East Tamar), 5 (North –east), 6 (Central plateau), 7 (Northern midlands), 8 (South-west), 9 (Derwent valley), 10 (East coast), 11 (Southern forests), 12 (King Island).

Traits

At age six years the trial was measured for the following: survival; growth traits - stem diameter at ground level, and tree height; and form traits - stem kink, stem count, stem form, branch size and butt length. Stem kink was assessed over the entire length of the main stem (1 = kinked, 0 = straight); stem count (0 = single stem, 1 = multi-stem); stem form was subjectively scored on a 9 point scale (1 = bush, 2 = 1 m of single straight stem at base, 3 = extremely kinked throughout, 4 = kinked lower half, 5 = kinked top half, 6 = heavy branching but minor kinks, 7 = kinked top third, 8 = kinked in recent growth, 9 = perfect single straight stem); branch size was visually assessed on a three point score (1 = branches mostly < 0.5 cm diameter, 2 = branches 0.5 – 2.0 cm diameter, 3 = branches >2.0 cm diameter); and butt length (percentage of total tree height from the ground to the first kink on the main stem). Stem kink was defined as the loss of apical dominance in the main stem and subsequent replacement by one or more leaders, resulting in a displacement to the main stem exceeding the diameter of the stem at the point of kink.

Analysis

The significance of the seed zone and family-within-seed zone effects was tested by fitting a linear mixed model:

Equation 3.1: $Y = \text{MEAN} + \text{REP} + \textit{IBLK} + \text{SEEDZONE} + \textit{FAM(ZONE)} + \textit{PLOT} + \textit{ERROR}$

where Y is a vector of observations; MEAN is the trait mean; REP are fixed replicate effects; *IBLK* are random incomplete block within replicate effects; SEEDZONE are fixed zone-of-origin effects; *FAM(ZONE)* are random family within-seed zone effects,

PLOT are random plot within family effects and *ERROR* is a vector of random within-plot residuals. Quantitative traits were modelled using Proc MIXED of SAS (ver. 9.1, SAS Institute Inc. 2004) and presence/absence traits were modeled with ASREML (Gilmour *et al.* 2006) using a binary model with a probit link function. Differences between seed zones were tested with an F-test using *FAM(ZONE)* as the error term. Z-tests were used to test the significance of random terms. For the analysis, the single family from seed zone 7 was included in the nearby seed zone 5. Families were compared on the basis of their best linear unbiased predictions (BLUPs) derived from an analysis in which the seed zone effect was removed from Equation 3.1. The unbalanced distribution of some families across the trial is unlikely to bias the BLUP estimates as both incomplete block and family effects are treated as random effects in the model and thus should be simultaneously estimated.

The effects of changes in the seed collection strategy from "phenotypically superior" to "random" were tested by including the term YEARGROUP as a fixed effect in the mixed model in SAS, where YEARGROUP was the collection dates grouped into the two classes 1988-89, and 1991-93. The effect of the altitude from which the seed was originally collected was tested by including maternal tree altitude as a covariate in the same mixed model analysis. Neither YEARGROUP nor altitude was found to have a significant effect on blackwood growth or form.

Where significant seed zone effects were identified, a Tukey-Kramer test for multiple comparisons was used to identify a significant difference at $p < 0.05$. Narrow-sense heritabilities (h^2) were calculated by fitting the same model as above without the additional covariates with ASReml assuming full outcrossing and a half-sib model, as:

Equation 3.2: $$h^2 = \frac{4 \times \sigma^2_{family(zone)}}{\sigma^2_{family(zone)} + \sigma^2_{plot} + \sigma^2_{residual}}$$

where $\sigma^2_{family(zone)}$ is the family within seed zone variance component, σ^2_{plot} is the random variation between plots of the same family, and $\sigma^2_{residual}$is the residual variation (Williams *et al.* 2002).

The assumption of full outcrossing is based on the high outcrossing rates of 0.86 and 1.0 reported for two native blackwood populations (Muona *et al.* 1991), and the half-sib model used assumes a coefficient of relatedness of 0.25 amongst sibs. This heritability calculation also assumes random mating within seed zones with females sharing a common pollen pool (Williams *et al.* 2002). Genetic and environmental correlations were calculated among untransformed traits scored from the family trial by fitting Equation 3.1 in a bivariate analysis, using ASReml (Gilmour *et al.* 2006). The genetic correlations were derived from the variance and covariance components amongst families within seed zones (Jordan *et al.* 1999). Z-tests were used to determine whether correlations differed significantly from zero. Standard errors of heritabilities and genetic correlations were derived using a Taylor series with ASReml (Gilmour *et al.* 2006).

Results

Survival and Growth

Good browsing and weed control at the Oigles Road trial helped achieve high survival after six years. There were no significant seed zone or family(zone) effects for survival and the heritability estimate was low (Table 3.2). Growth rates across the trial varied with replicate means ranging from 6.8 cm to 9.4 cm for diameter, and from 266 cm to 379 cm for height, with a strong site trend for increasing growth down-slope. There was a significant seed zone effect on height but not on diameter (Table 3.2). This seed zone effect was due to the average tree heights in families from the Far North-west and West coast seed zone (1) being significantly greater than those from the East Tamar seed zone (4) (Figure 3.2).

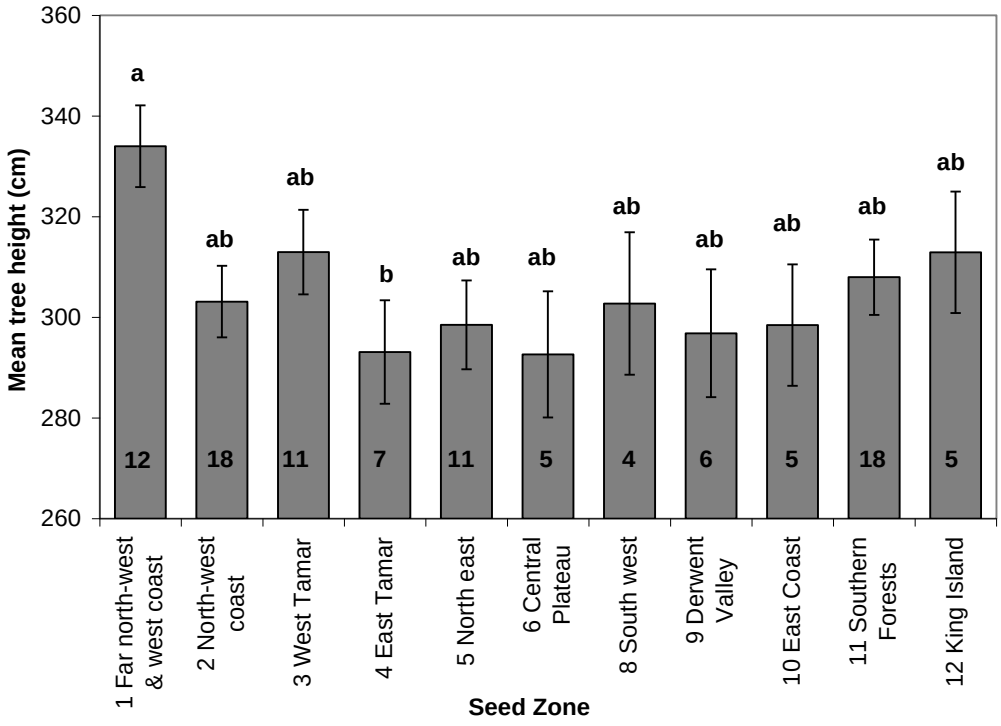


Figure 3.2: Mean tree height at age 6 years by seed zone with standard error bars, number of families per seed zone (in bold in each bar) and results of Tukey-Kramer pairwise comparison. Seed zones with the same letter are not significantly different at p <0.05. Seed zone 11 (Southern Forests) was the local seed zone.

Families from the Southern Forests seed zone (11), within which the Oigles Road trial was located, were not significantly different in height growth from the other, non-local, seed zones. Family within seed-zone effects were significant for height (p <0.001) and diameter (p <0.01) (Table 3.2), with individual heritabilities estimated to be 0.33 and 0.26, respectively. Family BLUPs (estimated with seed zone removed from the model) for diameter and height identified a group of families exhibiting outstanding height and/or diameter growth as well as a group of poorly performing families (Figure 3.3). The four families with outstanding growth came from seed zones 1 (2 families), 2 and 10, whilst the five worse performing families came from seed zones 2, 3, 4, 5 and 10.

Table 3.2: Summary statistics and results of a mixed model analysis testing between seed zones and families within seed-zones effects; and narrow sense heritability estimates. Seed zones are given in Figure 3.1. Stem kink and stem count are binary traits.

Trait	N	Mean	Std Dev	Seed Zone $F_{10,91}$ value	Family(Zone) Z value	Heritability h^2	*se*
Survival (%)	1839	90	30	1.31	0.58	0.06	0.112
Diameter (cm)	1657	7.77	2.60	1.72	3.07**	0.26	0.081
Height (cm)	1657	308	81	2.10*	3.22***	0.33	0.098
Stem kink	1839	0.86	0.35	0.96	1.36	0.15	0.107
Stem count	1657	0.69	0.46	1. 66	0.64	0.05	0.075
Branch size	1655	2.15	0.83	1.13	2.70**	0.22	0.077
Stem form	1656	4.24	1.37	1.63	1.67*	0.10	0.059
Butt length (%)	1657	36	26	1.74	2.90**	0.21	0.068

Indicates significant diference at p <0.05, ** p <0.01, *** p <0.0001.

Form

All form traits reflected the poor form of open-grown, unpruned blackwood. High incidences of both stem kinking and multi-stems were found across the trial, while branch size was generally between medium (2) to large (3) (Table 3.2). Stem form was

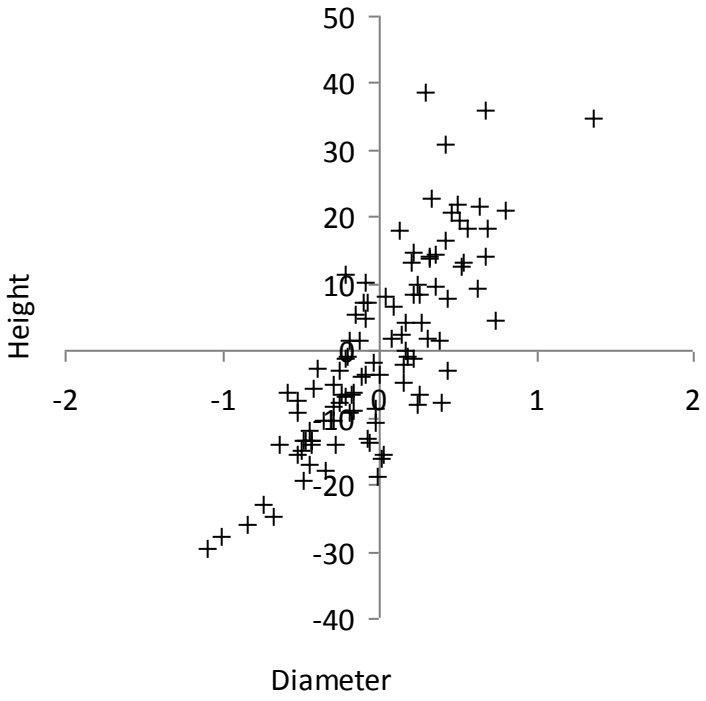
generally poor, and the mean butt length was only 36% of total height (Table 3.2). Form traits did not show significant seed-zone effects. However, branch size, butt length (p <0.01) and stem form (p <0.05) did show significant family within seed-zone effects, with heritabilities ranging from 0.1 to 0.22 (Table 3.2). Form traits were generally less heritable than growth traits.

Table 3.3: Genetic family within seed zone (below the diagonal with standard errors) and phenotypic (above the diagonal with *p* values) correlations (*r* values) amongst growth and form traits (genetic correlations in bold are significant at *p*<0.05).

	Diameter	Height	Branch size	Stem form	Butt length
Diameter		0.83 <0.0001	0.72 <0.0001	-0.05 0.06	-0.09 0.0002
Height	**0.74±0.093**		0.58 <0.0001	0.15 <0.0001	0.06 0.01
Branch size	**0.84±0.095**	**0.34±0.20**		-0.15 <0.0001	-0.18 <0.0001
Stem form	-0.20±0.31	0.40±0.27	**-0.59±0.30**		0.46 <0.0001
Butt length	-0.29±0.23	0.18±0.22	**-0.50±0.22**	**0.80±0.17**	

All traits studied were significantly inter-correlated at the phenotypic level and most of the higher phenotypic correlations were also expressed at the genetic level (Table 3.3). Diameter and height were significantly strongly positively correlated at both the genetic (i.e. family within seed zone) and phenotypic (i.e. tree) level (see also Figure 3.3 for family across seed zone correlations). Among the form traits, stem form and butt length were strongly positively correlated at the genetic level and both were strongly negatively correlated with branch size. Similar but less marked trends were also evident at the phenotypic level. Branch size was positively correlated with diameter and height at the genetic and phenotypic levels. At the phenotypic level stem form and butt length were weakly positively correlated with height and

a)



b)

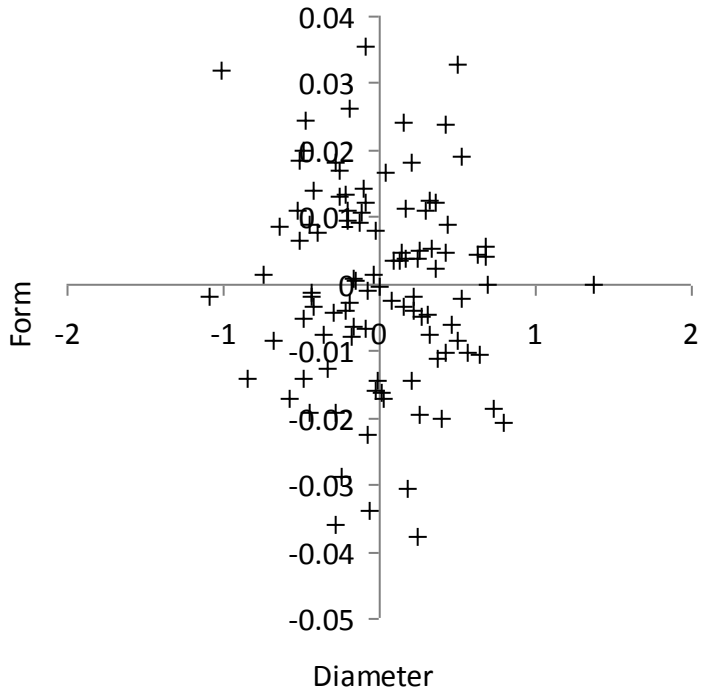


Figure 3.3: Scatter plots of family BLUPs (calculated over seed zones) for diameter against height (a), and form (b).

negatively with diameter, but while of the same direction these correlations were not significant at the genetic level (Table 3.3). Across all seed zones, family BLUPs for stem form showed no relationship to stem diameter (Figure 3.3), and the most outstanding family for diameter had near average form.

Discussion

The good survival in the trial was due in part to good early control of mammal browsing and weeds. Growth, as measured by stem diameter and height, was generally poor, only approaching commercial growth rates (>1.5 cm yr^{-1} diameter increment) towards the lower end of the trial (Nicholas and Brown 2002; Berrill *et al.* 2007). There was relatively little differentiation in height growth between the seed zones, with a significant difference only between the tallest and shortest zones. In an 18-year-old trial in north-west Tasmania testing 37 open-pollinated blackwood families, families from north-east Tasmania had significantly greater diameter growth than those from south-east Tasmania (Chapter 4). However, this trend was not detected in the larger collection of families tested at the Oigles Road trial. While there was little differentiation between seed zones detected in the present study, families from the far north-west and west coast of Tasmania (seed zone 1) had the best growth. The apparently different results from these two studies may be due to i) changes in growth with age, ii) genetic by environmental interaction, or iii) sampling different seedlots. Significant age-age correlations were found between early-age height and later-age diameter in three blackwood trials (Chapter 4) suggesting that changes in growth with age may not be responsible for the different performance in growth between seed zones in the two studies. Similarly no significant genetic by environmental interaction effect on stem diameter was found in 16 families common across three 18-year-old trials (Chapter 4).

The different results between the two studies may be due to different samples of families, although 22 families were common between the two trials.

A key issue in both native forest silviculture (Matthews 1991) as well as restoration ecology (Broadhurst *et al.* 2008) is the consequences of the transfer of seed between different seed zones/regions. One of the arguments for use of local seed is that it is better adapted to the local environment (Potts and Wiltshire 1997), although issues of conservation of the natural patterns of genetic diversity and off-site genetic contamination (Potts *et al.* 2003), as well as responding to climate change (Rehfeldt *et al.* 1999) are also important considerations. In the present study, while exact on-site seed was not used, it was apparent that families from the local seed zone 11 (Southern Forests) did not provide any significant advantage in growth over families from the other seed zones. Indeed, family BLUPs for diameter and height, indicated that the small group of families of outstanding growth originated from a range of seed zones, none of which were the local zone. These results may reflect the fact that i) dispersal limitations have restricted the colonization of the local site by better adapted germplasm; ii) early growth rate is a poor indicator of either later age growth or reproductive fitness; or iii) local adaptation over steep environmental gradients within seed zones is more important than broad-scale geographic differences (Wilkinson 2008).

Most quantitative genetic variation in blackwood survival, growth and form resides within rather than between seed zones within Tasmania. These findings on genetic variation are consistent with those reported for other *Acacia* species (Harwood *et al.* 1993; Arnold and Cuevas 2003), while the low to moderate genetic control over growth and form traits in blackwood are also in line with other studies in acacias (Arnold and Cuevas 2003; Hai 2009). However the relatively low level of differentiation between

seed zones for growth and form is not supported by other studies. For example, *A. auriculiformis* (Hai 2009) and *A. mangium* (Lokmal *et al.* 1995; Faizuddin and Dalmacio 1996; Arnold and Cuevas 2003; Nirsatmanto *et al.* 2003) exhibit significant differences in growth and form within- and between-populations. The relatively low effect of seed zone on growth and form within Tasmanian blackwood may be due to either i) the young age and relatively slow growth in the Oigles trial preventing the expression of a greater variation to date, ii) the 12 seed zones do not adequately represent the existing variation, which may be expressed at a finer geographic scale, or iii) there is little broad-scale geographic variation in growth and form in blackwood within Tasmania. The original seed collection strategy of generally widely dispersed families rather than provenance-based collections on which the Oigles trial is based, means that the variation within seed zones cannot be partitioned into between- and within-local populations. It is also important to note that the geographic range of blackwood in the trial is only a portion of its total distribution across eastern Australia. Across this greater geographic range there is evidence of broad-scale differences in adaptation as demonstrated and discussed in Chapter 4.

Growth traits in blackwood in this trial were found to be more heritable than form traits. This trend was not consistent with Chapter 4 where growth and form trait heritabilities, calculated using a smaller (16) sample of older Tasmanian blackwood families, were more varied, and with form traits often more heritable than growth traits. Similarly studies in other acacias have produced varying estimates for both growth and form trait heritabilities (Hai 2009). However the present heritability estimates are within the range of values previously reported, despite the potential that the present

estimates are over estimated due to the broad-scale seed zones into which families were allocated.

Growth and form in blackwood are genetically independent in the present study while studies in other *Acacia* species have shown positive genetic correlations between growth and form traits (Arnold and Cuevas 2003; Hai *et al.* 2008). At the environmental level these factors are probably positively related as exposure to weather and shelter have been reported as influencing both growth and form in blackwood (Neilsen and Brown 1996; Nicholas and Brown 2002). The Oigles trial is located on an upper west-facing slope with exposure to the prevailing westerly winds. This exposure together with the young age and relatively slow growth of blackwood may have prevented the expression of significant genetic correlations between growth and form. Indeed, at the phenotypic level there is a positive correlation between tree height and stem form and the same non-significant trend was evident at the genetic level.

A better understanding of the various factors affecting form is required to improve the management and production of sawn timber from blackwood plantations. Poor stem form observed in the trial appears to be a common feature amongst acacias, with various possible causes cited including grazing from ungulates or insects, site quality, genetics, stand composition, exposure or some combination of these factors (Neilsen and Brown 1996; Appleton *et al.* 1997; Nicholas and Brown 2002; Jennings *et al.* 2003; Baker *et al.* 2009). Nevertheless this study shows that there is genetic variation in form traits, which at least at this site is independent of genetic variation in growth traits and improvement in both traits should be possible by selection. However, these results are based on only a single trial, and while no significant family by site interactions were detected for latter age growth and form in a limited sample of blackwood families across three trials in

northern Tasmania (Chapter 4), this issue clearly requires further exploration using more diverse germplasm and planting sites. In addition, wood properties as well as growth and form are important in affecting blackwood value (de Zwaan 1982; Harington 2007). There is significant genetic variation in wood properties, as reported in Chapters 6 and 7, and Nicholas *et al.* (1994b; 2007), which also needs to be considered.

Conclusion

This study has revealed significant genetic variation for growth and form traits in blackwood, and at least in Tasmania, this variation appears to mainly reside within rather than between seed zones. Growth was under stronger genetic control than that of form traits, and both appear to be amenable to independent genetic improvement. However, such improvement will require a better understanding of the importance of site variation in the expression of this genetic variation.

Chapter 4: Genetic Control in the Later-Age Survival, Growth and Form of *Acacia melanoxylon*

Introduction

Australian blackwood (*Acacia melanoxylon* R.Br.) occurs in eastern Australia over a wide latitudinal range from north Queensland (16°S) to southern Tasmania (43°S), and westwards into South Australia. It is one of the most wide-ranging tree species in eastern Australia, with considerable phenotypic (Farrell and Ashton 1978), and allozymic (Playford *et al.* 1993) variation. Increasing genetic variation with increasing latitude was found for four measures of genetic diversity, with most variation found within populations but unusually high levels of variation also between populations (Playford *et al.* 1993). Blackwood grows in a range of habitats, but favours fertile soils in valleys and on flats in mountainous areas, often growing in wet sclerophyll forest and cool temperate rainforest. Within Tasmania blackwood is widespread and common, ranging in altitude from sea level to over 1,000 m. In north-western Tasmania blackwood grows as a tall dominant tree in forested seasonal swamps (Cowan and Maslin 2001).

Acacias are predominantly outcrossing, but the breeding system of individual species varies from strongly self-incompatible to fully self-compatible (Kenrick *et al.* 1986; Kenrick and Knox 1989; Daehler *et al.* 1999; Kenrick 2003). Pollen of *Acacia* species is transported as polyads by a variety of vectors, with each polyad having enough pollen grains to fertilize all ovules within a flower. Hence all seed within a pod may be full sibs. In the case of *A. melanoxylon* a study of two native populations found that outcrossing rates varied between 0.86 and 1.0, and that the proportions of pods with

multiple paternity was between 0.08 and 0.15, i.e. most pods contain seed which are full sibs (Muona *et al.* 1991).

Within Australia blackwood timber is sourced from native forest harvesting operations. Blackwood has been introduced as a plantation species into many countries including South Africa, New Zealand, Vietnam, China and Chile. The latter two countries have active breeding and plantation programs (eg. Nicholas 2007c). Blackwood timber is of medium density (440 – 580 kg m^{-3}), with excellent drying and finishing properties. It has a pale cream sapwood colour with heartwood colour ranging from straw to golden brown to mahogany red and black walnut. It occasionally exhibits strong figure in the grain such as birdseye or fiddleback which is in strong demand (Bootle 2005).

However issues such as wide phenotypic variation, poor apical dominance, sensitivity to site, frost, and high susceptibility to animal browsing (e.g. New 1984), have caused problems in the domestication of blackwood. In spite of these potential problems blackwood can still be planted on a wide range of sites, although care is required if it is to be grown successfully as a commercial timber crop. Nicholas and Brown (2002) list shelter, moisture, soil type and freedom from frosts as the critical factors to consider in choosing planting sites if the best growth rates and form are to be realised. Diameter growth rates reported for blackwood in trials and plantations range between 0.2 – 4.3 cm yr^{-1}, with rates of >2.0 cm yr^{-1} not uncommon (Ryan and Bell 1991; Zhang *et al.* 1998). Reported height growth rates for blackwood range from 0.3 – 4.0 m yr^{-1} with rates of 0.6-1.0 m yr^{-1} being commonly recorded.

Numerous studies in plantations (Neilsen and Brown 1996; Searle *et al.* 1998; Stackpole 2001; Medhurst *et al.* 2003; Pinkard 2003; Pinkard and Neilsen 2004;

Medhurst *et al.* 2006) and native forest regeneration (Unwin *et al.* 2001; Jennings *et al.* 2003; Jennings 2004; Unwin and Jennings 2007) have demonstrated that blackwood growth and form is highly sensitive to the ambient light environment. As available light increases height growth decreases, while green crown depth, the incidence of large branches, and diameter growth increase, and apical dominance is progressively lost. This loss of apical dominance has been shown to be due in part to insect damage (Appleton *et al.* 1997).

Silvicultural research in New Zealand has resulted in the development of blackwood plantation regimes that feature intensive form and lift pruning that control branch size and enhance the development of single straight stems (Nicholas and Brown 2002). Silvicultural research in Tasmania has focused on i) blackwood plantations using nurse crops together with pruning to control form and branching (Medhurst *et al.* 2003; Pinkard 2003; Pinkard and Neilsen 2004; Medhurst *et al.* 2006), and ii) manipulation of native forest silvicultural regeneration to control blackwood form whilst improving growth rates (Jennings *et al.* 2000; Unwin *et al.* 2001; Jennings *et al.* 2003; Jennings 2004; Pinilla and Briones 2007; Unwin and Jennings 2007).

In contrast to silvicultural research, there has been little published on genetic variation within the species and how to exploit it. Although significant differences in growth between provenances have been observed previously (de Zwaan and van der Sijde 1990; Appleton *et al.* 1997; Searle 1998; Searle *et al.* 1998; Zhang *et al.* 1998; Stackpole 2001; Jackson *et al.* 2004; Zhang *et al.* 2004), many trials have had limited numbers of seedlots, often collected from a wide geographic and climatic range with little replication. Between 1988 and 1993 blackwood seed collections were made and a number of progeny trials established in Tasmania (Chapter 2; Allen 1992; Neilsen and

Brown 1996). Early-age measurements from these trials are reported by Neilsen and Brown (1996). Interest in these progeny trials then waned until a recent review of available blackwood genetic resources (Chapter 2) identified several of these trials as an important resource for later-age assessment. The objective of this study was thus to test for genetic effects on later-age survival, growth, and form of blackwood in progeny trials in Tasmania.

Materials and Methods

Trials

This study used five blackwood progeny trials at two locations, Meunna and Virginstow, in northern Tasmania, Australia, established between 1988 and 1992 (Figure 4.1, Table 4.1) (Allen 1992; Neilsen and Brown 1996). The trials were all planned as randomised complete replicate designs, but seedlot limitations and site constraints in trials Meunna 266/2/2 and Virginstow 266/4/2 meant that not all families were represented in all replicates and it was necessary to split replicates into adjoining planting bays (treated as different blocks in the analysis). Trials differed in plot size. Three trials were pure blackwood plantings (Meunna 266/1/2, Meunna 266/2/2, and Virginstow 266/4/2) with families represented as line plots of 20 trees in each replicate. The remaining two trials were mixed blackwood and nurse crop plantings. Nurse crops were included as they were expected to enhance blackwood survival and form. In nurse crop trial Virginstow 266/4/1, families were planted in plots approximately 0.2 ha in area with alternate rows of blackwood and nurse crop, with a minimum of seven rows of blackwood per plot. In nurse crop trial Meunna 266/6, families were planted as 10 tree line plots planted alternately with rows of nurse crop. The three trials at Meunna were

located on good sites with deep fertile soils and high rainfall. The two trials at Virginstow were located on a site with lower rainfall and poor soils.

Neilsen and Brown (1996) noted that all trials except Meunna 266/6 were subjected to browsing and weed competition during early establishment, and significant frost damage occurred at Meunna. All three factors were anticipated to affect the survival, growth and form of the blackwood. At Meunna 266/6, 1.2 m-tall plastic grow tubes protected the seedlings from frost and browsing damage.

Genetic Material

A total of 56 Tasmanian families were represented across the five trials (Table 4.2). The number of families planted in each of the trials differed (Table 4.1). One trial (Meunna 266/1/2) contained seven bulk seedlots from mainland Australian provenances supplied by CSIRO's Australian Tree Seed Centre, Canberra (Table 4.3). The Tasmanian seedlots were open-pollinated single-tree family collections made between 1988 and 1991 from around the State, encompassing all of the 12 blackwood seed collection zones defined by Allen (1992) (Figure 4.1, Table 4.2). Tasmanian collections made in 1988-89 were from single trees of superior form, while later collections were from randomly selected trees (Neilsen and Brown 1996). Of the Tasmanian families, none were common to all five trials, three were common to four trials, 16 were common to three trials, four were common to two

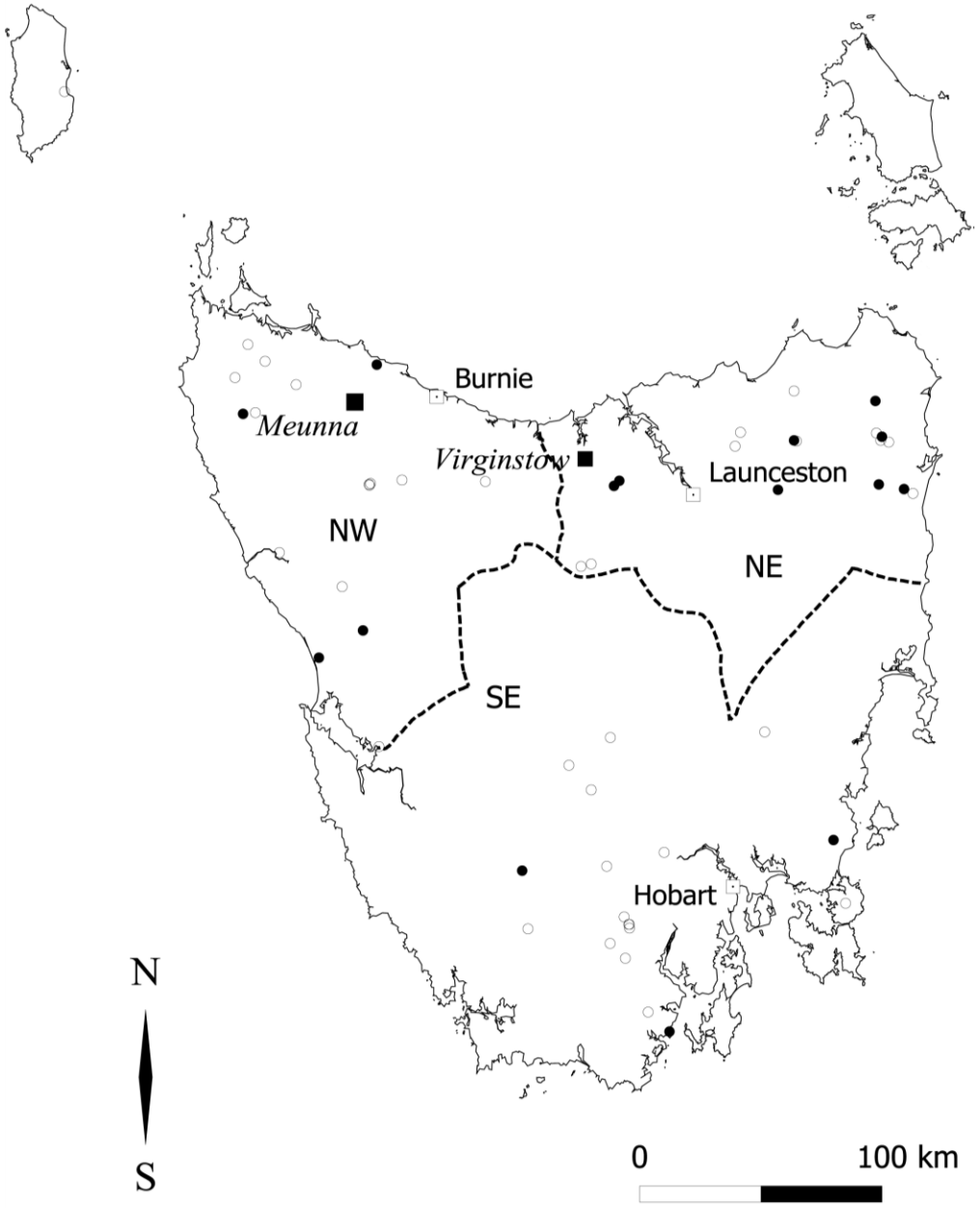


Figure 4.1: Tasmania showing the locations of blackwood trials (■), the collection sites of the Tasmanian single tree family seedlots (○) and those common to the three trials used in the study of genotype by environment interaction (●). The seed zones marked (- - -) correspond to north-west (NW), north-east (NE) and south-east (SE) Tasmania.

Table 4.1: Blackwood trial designs and attributes

Location	Meunna	Meunna	Virginstow	Virginstow	Meunna

Trial code	266/1/2	266/2/2	266/4/1	266/4/2	266/6
Year planted	1988	1989	1989	1989	1992
Latitude (°S)	41°05’		41°18’		41°05’
Longitude (°E)	145°28’		146°36’		145°28’
Altitude (m)	280	320	160	160	300
Number of Tasmanian families	16	37	17	17	14
Number of mainland provenances	7	0	0	0	0
Nurse crop	-	-	*E. globulus*	-	*E. nitens*
Replicates (measured 2007)	5 (5)	5 (3.3)	2 (2)	5 (5)	2 (2)
Trees per plot	20	20	80	20	10
Stocking [nurse] (stems.ha^{-1})	800	800	400 [800]	800	1111 [1111]
Spacing (m) (row x column)	3.8x3.29	4.2x2.98	4.2x5.96	4.2x2.98	1.5x6.00
Trial area (ha)	2.7	3.7	6.2	2.2	0.4
Replicates with historical data	3	1	-	3	2
Historical data age (yr)	1, 2, 6	6	-	6	3
Age when assessed in this study (yr)	18	17	17	17	14

Table 4.2: Summary of blackwood seedlots used in the five trials

Seed Zone	Altitude range (m)	Number of seedlots	Seedlots per Trial				
			Meunna 266/1/2	Meunna 266/2/2	Virginstow 266/4/1	Virginstow 266/4/2	Meunna 266/6
NW	5 - 520	19	8	10	5	5	7
NE	40 - 620	20	4	16	8	8	2
SE	1 - 440	17	4	11	4	4	5
Mainland	100 - 1120	7	7	0	0	0	0

Table 4.3: Details of blackwood seedlots from mainland Australia planted in Meunna 266/1/2

Code	Location	Parents	Altitude (m)	Latitude (°S)	Longitude (°E)
14176	Atherton, QLD	10	1022	17.28	145.43
14585	West of Brisbane, QLD	5	100	27.40	152.92
15371	10km WSW of Atherton, QLD	10	1000	17.30	145.42
17264	Springbrook, QLD	2	750	28.23	153.28
14428	Tallaganda, NSW	10	1120	35.42	149.52
15355	Otway Ranges, VIC	4	440	38.68	143.40
15614	Silver Creek, VIC	Unknown	240	38.37	146.25

trials, and 33 were found in only one trial. Both the genetic sampling strategy and the trial designs were not ideal, however they represent the best of the available genetic resources for mid-age blackwood genetic research (Chapter 2).

Traits

The following traits were recorded: survival (1 = present, 0 = dead/absent); growth, measured as stem diameter at breast height (1.3 m) over bark (DBHOB); and tree form, assessed using three traits. The three form traits were a) stem form (1 = very poor form with twisting and/or multiple leaders, to 4 = good with single stem) as detailed in Neilsen and Brown (1996), b) stem kink (1 = straight stem to 4 = stem deviates outside

centreline, after Medhurst *et al.* 2003) and c) large branch count i.e. number of branches with a diameter of >3 cm. All three form traits were only assessed within the lower 6 m of each tree, as current silvicultural regimes (eg. Nicholas and Brown 2002) involve only pruning the lower 6 m of each tree, hence this is the focus of commercial production. Kink was only assessed on trees scoring 4 for stem form (i.e. with a single stem). Trees that scored 1 for kink (single straight stem) were therefore potential sawlog trees (branches excluded). Due to low survival in parts of Meunna 266/1/2, only 3 of the 5 replicates were included in the analysis. Only 3.3 of the 5 replicates of Meunna 266/2/2 were assessed, as blackwood wildlings made planted individuals difficult to identify. Earlier measurement data was available for four of the trials, comprising height and survival, and was included in the analysis (Table 4.1).

Analysis

Both stem form and kink scores were converted to binomial classifications (Form: 0 = multiple stems and/or poor form, 1 = good single stem; Kink: 0 = single kinked stem, 1 = single straight stem). Data analysis was subsequently performed on plot means or proportional data. Proportional data was arcsine square root transformed. Branch count was log transformed. Transformations were necessary to satisfy assumptions of normality and homogeneous variances for the residuals. Plot basal area was calculated as the sum of the individual tree basal areas (dead = 0). The significance of seedlot on survival, growth and form traits within each trial was tested by fitting a mixed linear model to plot-level data using Proc MIXED of SAS (ver. 9.1, SAS Institute Inc. 2004). The model fitted was:

Equation 4.1: $Y = MEAN + REP + SEEDLOT + \mathit{ERROR}$

where REP is the replicate and SEEDLOT is the seedlot both fitted as fixed terms, and the *ERROR* term was the seedlot x replicate residual variation. An additional term *BLOCK(REP)* was included for trials Meunna 266/2/2 and Virginstow 266/4/2 to account for differences between blocks within replicates. With Meunna trial 266/1/2, which contained seedlots from different regions of Australia, a similar model was also fitted to test the effect of REGION (regions were Queensland, southern mainland Australia and Tasmania) as a fixed effect, with *SEEDLOT(REGION)* nested as a random term within region.

As Meunna 266/2/2 had the largest selection of Tasmanian families, a mixed linear model was also fitted to test the significance of seed zone (see Figure 4.1), altitude and seed zone by altitude interactions. The three seed zones used were an amalgamation of the 12 seed zones defined by Allen (1992) due to the low and uneven number of families per zone The model fitted was:

Equation 4.2: $Y = REP + ZONE + ALT + ALTxZONE + BLOCK(REP) + FAMILY(ZONE) + ERROR$

where REP is the fixed replicate effect, ZONE is the fixed effect of seed zone as defined in Figure 4.1. ALT is the altitude of the family collection site fitted as a covariate, and ALTxZONE is the interaction between altitude and seed zone; *BLOCK(REP)* is the incomplete block within replicate and *FAMILY(ZONE)* is the family nested within seed zone, both fitted as random terms in the model. Altitude was chosen as a covariate as the Tasmanian families were collected over a wide range of altitudes. The interaction term ALTxZONE was included to account for the possible differing responses to altitudinal variation in different seed zones. This model was also fitted excluding ALT

and ALTxZONE in order to calculate variance components for estimation of narrow-sense heritabilities. Narrow-sense heritabilities were calculated as four times the family-within-zone variance component divided by the phenotypic variance. The phenotypic variance was estimated as the sum of the family(zone), plot and residual variance components. These variance components were estimated by fitting the above model including a plot term to the individual tree data. Presence/absence traits were analysed using a binary model with a logit link function.. The model was fitted and heritabilities and their standard errors estimated using ASREML (Gilmour *et al.* 2006), The significance of the heritability estimates from zero was tested using a Z test.

To test for genetic by environmental interactions, plot-level data for a set of 16 Tasmanian families common across three trails (Meunna 266/2/2 and Virginstow 266/4/1 and 266/4/2) were tested with the mixed linear model:

Equation 4.3: $$Y = TRIAL + FAMILY + TRIALxFAMILY + REPLICATE(TRIAL) + ERROR$$

where TRIAL is the fixed effect of trial, FAMILY is the fixed effect of Tasmanian family seedlot, TRIALxFAMILY is the fixed interaction term, and *REPLICATE(TRIAL)* is the random replicate effect nested within each trial. In testing the significance of family on large branch count, stem diameter was included in the above model as a covariate, to allow for the possible correlation between large branch count and stem size.

When a significant FAMILY or REGION effect was detected within the mixed model analyses, the Tukey-Kramer test for multiple comparisons was used to determine which treatments were significantly (p <0.05) different. Pearsons correlation tests using

seedlot-level data were performed on all trials using SAS Proc CORR to test for correlations between traits. SAS Proc REG was used to test the significance of age-age regressions and the relationship between family mean performance and altitude.

Results

Survival

Blackwood survival at ages 14-18 years was relatively uniform across four of the five trials (Table 4.4). The one notable exception was Meunna 266/6 where plastic grow tubes had been used; survival was 90% at age 14 years. A comparison of later age with early age survival (Table 4.4) showed that most mortality had occurred by age 6 years. Significant differences in survival between blackwood seedlots were found in three of the five trials. In trial Meunna 266/1/2, the significant difference ($F_{22,36}$ = 11.1, p < 0.001) was due to the four Queensland provenances having significantly lower survival (3±0.01 %) compared with three New South Wales/Victorian provenances (66±0.10 %) and 16 Tasmanian family seedlots (84±0.02 %). There were significant differences in survival between the Tasmanian families in trials Meunna 266/2/2 ($F_{36,59}$ = 2.81, p =0.0002), and Virginstow 266/4/2

($F_{16,55}$ = 2.64, p = 0.004). The two trials with nurse crops showed no significant differences in survival between families. Survival was significantly correlated with diameter in two trials (Meunna 266/1/2 and 266/6), plot basal area in four trials (Meunna 266/1/2, Meunna 266/2/2, Viginstow 266/4/1 and Virginstow 266/4/2), percentage single stems in two trials (Virginstow 266/4/2 and Meunna 266/6), and large branch count in Meunna 266/1/2 (Table 4.5).

Table 4.4: Mean and standard deviation (in parentheses) for measured and derived traits for the five blackwood trials, and levels of significance[1] of the effect of seedlot. Survival includes early-age and later-age data, tree height is early-age data, while all remaining traits show later-age data only. For the two trials incorporating a nurse crop, the mean basal area of the nurse crop at 14 and 17 yrs is given.

Location	Age (yr)	Meunna 266/1/2	Meunna 266/2/2	Virginstow 266/4/1 (nurse crop)	Virginstow 266/4/2	Meunna 266/6 (nurse crop)
Survival (%)	1	95**				
	2	77***				
	6	65***	78*		63	95
	14-17	65***	66**	60	55**	90
Tree height (cm)	1	60*** (17)				
	2	85*** (34)		-		
	6	308*** (120)	333 (73)		300 (87)	220 (109)
Mean stem diameter (cm)	14-17	18.7*** (6.5)	13.7*** (5.8)	10.2 (4.4)	12.4** (5.3)	8.6* (3.2)
Mean annual diameter increment (cm yr^{-1})	14-17	1.04 (0.36)	0.83 (0.34)	0.63 (0.26)	0.75 (0.31)	0.60 (0.21)
Mean basal area (m^2 ha^{-1}) Blackwood, nurse	14-17	8.0*** (5.3)	4.8*** (2.9)	2.4, 24.9 (0.79, 4.8)	3.3*** (1.6)	7.2, 34.5 (2.4, 6.0)
Single stems (%)	14-17	49* (25)	72*** (24)	72 (19)	54 (26)	94* (10)
Single straight stems (%)	14-17	2.0 (6.4)	1.7 (3.1)	3.4 (4.5)	2.9 (7.8)	9.5 (12.5)
Large branch count	14-17	2.9** (1.2)	5.3* (3.4)	4.2 (2.9)	5.5* (3.1)	1.4 (1.4)

Significance levels are: * $p < 0.05$, ** $p < 0.01$, *** $p < .001$.

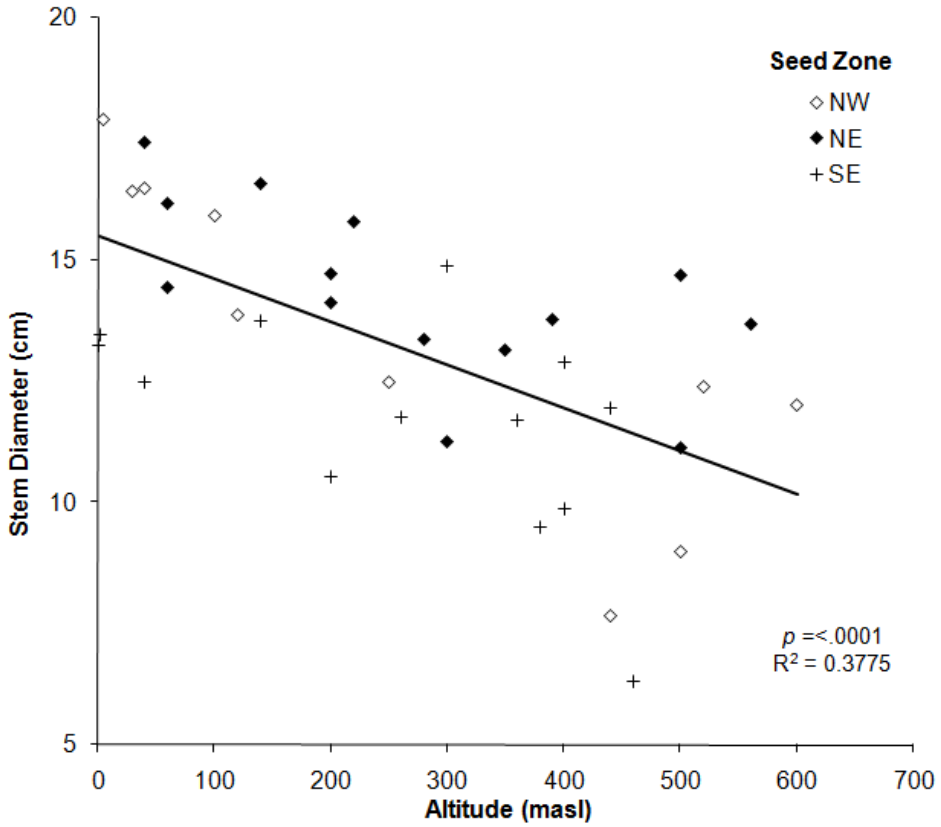


Figure 4.2: Ordinary least squares regression of family mean stem diameter by seed source altitude (metres above sea level) at age 17 yr for Tasmanian seedlots in Meunna 266/2/2. Seed zones are shown in Fig. 4.1.

Growth

Blackwood mean diameter growth rates were moderate across the five trials (Table 4.4). The two trials with nurse crops recorded the lowest mean diameter growth rates. Mean plot basal areas were likewise low across all trials due to either low survival and/or moderate growth. There were significant differences in growth rate between blackwood seedlots (Table 4.4). In Meunna 266/1/2 there was a highly significant difference in later age diameter between seedlots ($F_{22,36}$ = 5.3, p <0.001). The surviving trees from mainland provenances from New South Wales and Queensland, together with two south-east Tasmania (Sandspit 10A and Murdunna 10B) families, all had significantly lower growth rates than the remaining Tasmanian families and Victorian provenances. Significant differences in growth rates of surviving

trees were also found between Tasmanian families in three of the remaining four trials (Meunna 266/2/2, and Virginstow 266/4/1 and 266/4/2). The difference in growth rate amongst Tasmanian families could be partly explained by significant altitude and seed-zone effects. In the case of Meunna 266/2/2 which had the largest number of Tasmanian families, the mixed model fitted showed significant effects of altitude ($F_{1,58}$ = 25.0, p<.0001) and seed zone ($F_{2,32}$ = 3.58, p = 0.040) on the diameter growth of seedlots. There was no significant interaction between altitude and seed zone ($F_{2,58}$ = 0.74, p = 0.48). The diameter growth of the family decreased with increasing altitude of origin (Figure 4.2). Families from the south-east of Tasmania had significantly poorer diameter growth (mean diameter breast height at age 17 yr = 11.7±0.45 cm) than those sourced from the north-east (mean DBH = 14.6±0.47 cm), while those from the north-west had intermediate growth rates (mean DBH = 13.5±0.77 cm).

Table 4.5: Narrow-sense heritabilities, and Pearsons correlation (*r*) amongst traits based on seedlot-level data. The narrow-sense heritabilities (± se) and r values (above) with significance levels (below) for Meunna 266/2/2 which had the greatest number of seedlots is indicated below the diagonal. Above the diagonal, the r-value range across those trials where correlations were significant at $p \leq 0.05$, is given with the trials (a) where correlations are significant indicated in parenthesis.

	Heritabilities (h^2)	Survival	Stem Diameter	Basal area	Single stems	Single straight stems	Large branch count
Survival	0.82±0.33		-0.65 - 0.53	0.51 - 0.84	0.54 - 0.67	-	0.52
	**		(1,5)	(1-4)	(4-5)		(1)
Mean stem diameter	0.38±0.15	0.16		0.67 - 0.91	0.35 - 0.76	0.40 - 0.58	0.76 - 0.83
	**	ns		(1-5)	(1-4)	(2-3)	(1-4)
Mean basal area		0.51	0.87		0.37 - 0.64	0.44	0.57 - 0.63
		***	***		(2-4)	(2)	(1-4)
Single stems	0.84±0.41	0.22	0.35	0.37		0.59 - 0.63	-
	*	ns	*	*		(2-3)	
Single straight stems	0.36±1.31	0.19	0.40	0.44	0.59		-
	ns	ns	*	**	***		
Large branch count	0.03±0.08	0.16	0.83	0.63	0.08	0.20	
	ns	ns	***	***	ns	ns	

a. Trial codes are: 1 – Meunna 266/1/2, 2 – Meunna 266/2/2, 3 – Virginstow 266/4/1, 4 – Virginstow 266/4/2, 5 – Meunna 266/6.

b. Significance levels are: ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Pearsons correlation analysis showed that the plot mean diameter of surviving trees was both significantly negatively (Meunna 266/6) and positively (Meunna 266/1/2) correlated with plot survival in two trials, and significantly positively correlated with plot basal area in all five trials, percentage of single stems in four trials (Meunna 266/1/2, Meunna 266/2/2, Virginstow 266/4/1 and Virginstow 266/4/2), percentage of single straight stems in two trials (Meunna 266/2/2 and Virginstow 266/4/1) and large branch count in four trials (Meunna 266/1/2, Meunna 266/2/2, Virginstow 266/4/1 and Virginstow 266/4/2) (Table 4.5). For the three trials where age 6-year height data were available, regressions analysis showed that family means for early-age height was a significant predictor of mid-age (17-18 years) diameter growth (Figure 4.3).

Form

The percentage of trees with single stems at the five trials ranged from 49% to 94% (Table 4.4). At both Meunna and Virginstow sites the trial with nurse crop had the highest percentage of single stem trees. Significant differences in percentage of trees with single stems between seedlots were found at Meunna 266/1/2 ($F_{22,36} = 2.17$, $p = 0.019$), Meunna 266/2/2 ($F_{36,59} = 3.78$, $p < 0.0001$) and Meunna 266/6 ($F_{13,26} = 2.54$, $p = 0.021$). Form was significantly and positively correlated with diameter and basal area in three trials, and survival in two trials (Table 4.5). The percentage of trees with single straight stems in the first 6 m was very low across all trials except Meunna 266/6

where 9.5% of trees with a single stem had no kink (Table 4.4). There was a trend for faster growing seedlots to have a higher percentage of trees with single straight stems (Table 4.5). However no significant differences between seedlots were detected (Table 4.4). The mean number of large branches in the lower 6 m of the trunk varied between trials from 1.4 to 5.5 (Table 4.4) with the trials planted with nurse crops having lower branch counts. The number of large branches was positively correlated at the family level with diameter and basal area in four trials, and survival in one trial (Table 4.5).

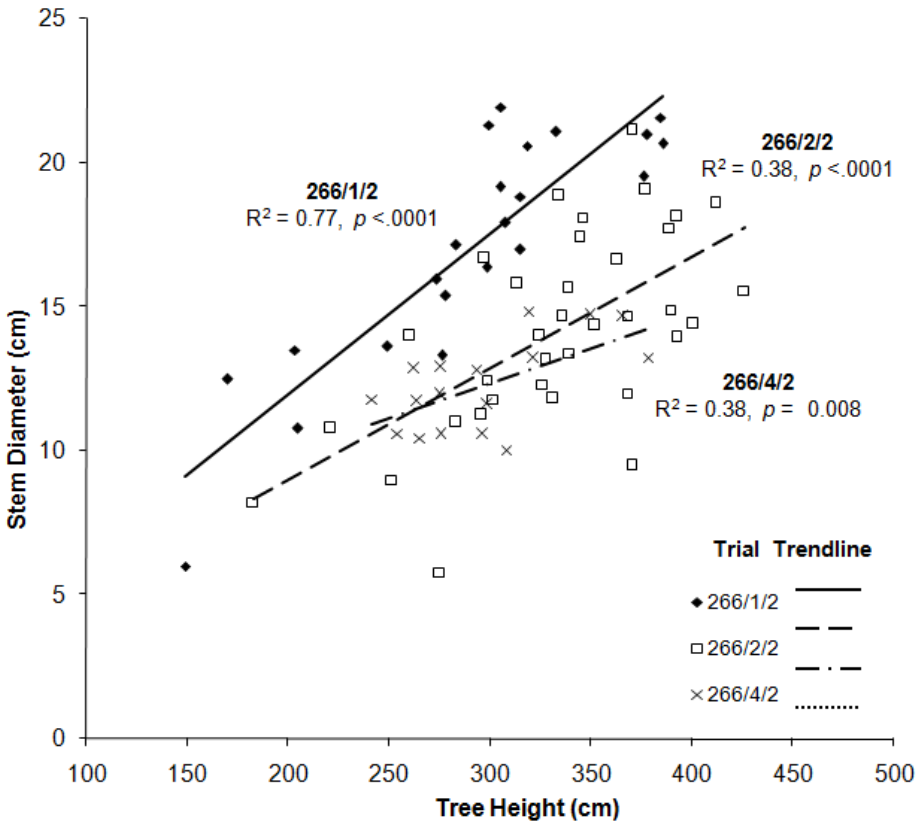


Figure 4.3: Ordinary least squares regression using seedlot-level data of early-age height against mid-age diameter. Trial Meunna 266/1/2 ht at age 6 yr, diameter at age 18 yr; Meunna 266/2/2 and Virginstow 266/4/2 ht at age 6 yr diameter at age 17 yr.

Table 4.6: The results of the mixed model analysis of genotype by environmental interactions using plot-level data for 16 Tasmanian family seedlots common across three trails (Meunna 266/2/2, Virginstow 266/4/1, and Virginstow 266/4/2)

Trait	Trial		Seedlot		Family x Trial	
	$F_{2,8}$ value	Prob	$F_{15,105}$ value	Prob	$F_{30,105}$ value	Prob
Survival	1.39	0.303	3.19	0.0002	0.99	0.500
Mean stem diameter	2.89	0.113	3.50	<0.001	0.57	0.960
Plot basal area	5.61	0.030	3.99	<0.001	1.48	0.077
Single stems	3.47	0.082	2.15	0.013	0.91	0.604
Single straight stems	1.08	0.385	1.30	0.217	0.64	0.915
Large branch count	1.75	0.234	2.43	0.004	0.70	0.871
Large branch count with mean stem diameter as covariate	2.53	0.149	0.59	0.871	0.91	0.592

Within the Tasmanian seed zones, the heritabilities for survival, stem diameter and presence of single stems were significant, with survival and presence of single stems in particular having high heritability estimates (Table 4.5). For the subset of 16 families common across three trials (Meunna 266/2/2, and Virginstow 266/4/1 and 266/4/2), no significant family by environmental interaction was detected for any of the traits assessed (Table 4.6). The trial effect was significant for plot basal area, while seedlot was significant for survival, diameter, basal area, the percentage of single stems, and the number of large branches. Once mean stem diameter was fitted as a covariate in the

model, the number of large branches was no longer significant at the seedlot level, reflecting the strong correlation between branch size and stem diameter.

Discussion

The objective of this study was to test for genetic variation in later-age survival, growth, and form of blackwood. Significant genetic effects on survival, growth and form were found both at the broad-geographic scale as well as within seed zones within Tasmania, but in the subset of germplasm examined across three Tasmanian trials, no genetic by environmental interaction could be detected.

Survival stabilized at an early age, with little subsequent mortality through to mid-age. Neilsen and Brown (1996) in discussing early results from the trials used in this study found that survival and tree height were significantly and positively correlated. They concluded that good height growth was necessary to enable the trees to get above the browsing and/or frost damage that were contributing to mortality. They also observed better blackwood survival under nurse crops than in pure blackwood plantings in an adjacent silvicultural trial at Meunna, perhaps reflecting improved protection from frost damage afforded by nurse crops.

The wide geographic and ecological range of blackwood within Australia provides opportunities for selection from a wide range of material for planting. However this and other studies indicate that care is required in matching planting material with site, particularly if the objective is commercial wood production. The requirement for the broad-scale matching of seed source and ecological/climate zone (Booth 1996) is clearly exemplified by the results from Meunna 266/1/2, where Queensland seedlots were

poorly adapted to the Tasmanian conditions in terms of both survival and subsequent growth of survivors. Broad-scale adaptive differences are particularly important given blackwoods' wide ecological and geographic range, and can significantly impact on performance. For example, Zhang *et al*. (2004) found Queensland and New South Wales (NSW) provenances of blackwood had significantly higher survival in high-rainfall tropical China than more temperate provenances from Victoria and Tasmania. Conversely, Stackpole (2001) and Searle (1998) found Queensland provenances had poor survival at trials in the colder climates of Victoria and the Australian Capital Territory, respectively. Franklin (1987) observed differences in survival within 30 provenances of blackwood after frost damage in New Zealand, with those from Tasmania exhibiting better frost tolerance than those from further north in Victoria or NSW.

At the regional scale at least within Tasmania, this simple seedlot-to-climate matching becomes more complicated. Genetic-based differences in survival and growth amongst Tasmanian families were evident in four of the five trials. In contrast to the study of *Acacia crassicarpa* in the Philippines where provenances with the best growth also had the best survival (Arnold and Cuevas 2003), there was no clear association between seedlot survival and the growth (DBH) of survivors in the present study although plot-level survival and basal area were significantly positively correlated in four of the five trials. For Tasmanian families there were significant differences in diameter growth that were associated with their region of geographic origin, and negatively associated with the altitude of collection of the seed source. Neilsen and Brown (1996) in these trials, and Jackson *et al.* (2004) in Victorian trials, both observed

negative correlations between early-age tree height and the altitude of provenance collection. These differences suggest adaptive trends in blackwood, for example where lower altitude sources had better growth at the low-to-mid altitude sites of these trials. However local seed sources at a regional level were not necessarily those that had the best growth rates, with families from the north-east seed zone generally having the best diameter growth. A number of authors have recorded improved growth rates from non-local compared with local seed sources. Bey (1980) found that black walnut (*Juglans nigra*) from southern United States sources had better growth and survival than local sources, with planting material capable of being moved up to 320 km (200 miles) north without suffering significant frost damage. Potts and Wiltshire (1997) provide a review of the fitness of local gene pools of eucalypts and suggest superior growth rates may not necessarily equate to long term fitness for survival. An extension of this argument is that most progeny trials are assessed when relatively young; drought, frost and competition that often influence long term survival may not yet have had an effect. Disequilibrium between local gene pools and prevailing selection pressures may also account for the better growth of non-local seed sources. Disequilibrium could result from endogenous (inbreeding, genetic drift) or exogenous (climate change, pests) factors (Potts and Wiltshire 1997).

The analysis of early-age height with mid-age diameter growth showed that height at age 6 years is a reasonable indicator of diameter growth through to mid-age. Hai *et al.* (2008) also found strong positive genetic age-age correlations in growth traits in clonal trials of *Acacia auriculiformis* in Vietnam. Knowledge of this age-age trend will be

useful in making early selections for growth in genetics trials and breeding programmes (eg. Osorio *et al.* 2003; Leksono *et al.* 2006).

Significant differences in the percentage of single stems between seedlots were found in three of the five trials. In the absence of nurse crops only a small percentage (1.7 – 2.9%) of blackwoods developed single straight stems, with this frequency not affected by seedlot. The number of large branches in the lower stem was significant at seedlot level at Meunna 266/1/2, once the correlation between large branch count and mean stem diameter had been accounted for by including mean stem diameter as a covariate in the model. The relatively low branch count detected in Meunna 266/1/2, which did not have a nurse crop, may be due to the faster growth at this site leading to earlier crown closure and consequent branch death and decay. Several authors (Stackpole 2001; Jackson *et al.* 2004; Zhang *et al.* 2004) have also reported significant differences in form between provenances. The significant and positive correlation between single stems and DBH found in three of the five trials supports the findings of Stackpole (2001) and Jackson *et al.* (2004) that good growth rates improve form. Stackpole (2001) compared 25 provenance seedlots at two sites and Jackson *et al.* (2004) compared 21 seedlots at two other sites, all in Victoria, Australia. The low random incidence of trees with single straight stems has also been observed in *Acacia koa* by Daehler *et al.* (1999) who found substantial variation within families in trunk forking in a family trial at age 1 year, with occasional trees having single straight stems. These results confirm that unpruned, open-grown blackwood exhibit poor form, high incidences of kink and large branches. These results are consistent with previous research in plantations (eg. Neilsen and Brown 1996;

Nicholas and Brown 2002; Medhurst *et al.* 2003; Pinkard 2003; Pinkard and Neilsen 2004; Medhurst *et al.* 2006) and native forest regeneration (Unwin *et al.* 2001; Jennings *et al.* 2003; Jennings 2004; Unwin and Jennings 2007) which has shown that blackwood stem form, kink and branching are sensitive to competition from surrounding vegetation such as nurse crops, but at the expense of diameter growth.

Factors apart from competition and light that have been found or are suspected to contribute to poor form in blackwood include leaf miners (*Acrorercops sp*.) (Appleton *et al.* 1997), poor growth rates (de Zwaan and van der Sijde 1990; Stackpole 2001; Jackson *et al.* 2004), site factors (particularly lack of shelter) (Neilsen and Brown 1996; Nicholas and Brown 2002), and low stocking (< 1,111 stems ha^{-1}) (Pinilla and Briones 2007). Shi and Brewbaker (2004) have achieved straighter boles and less forking in *Acacia koa* plantings in Hawaii at a stocking of 6,600 stems ha^{-1}. Further research is warranted so that a more complete understanding of factors affecting blackwood form can be achieved.

The Meunna site was regarded as an excellent location for growing blackwood, with fertile soils and high rainfall. Commercial blackwood plantation rotation lengths of between 35 and 45 years have been proposed for cool temperate locations (eg. Neilsen and Brown 1996; Nicholas and Brown 2002) with a target mean tree diameter of 60 cm. This implies a minimum mean annual diameter increment of 1.3 cm yr^{-1}. While individual trees in the three Meunna trials exceeded this growth rate, mean annual diameter increments were well below the minimum required. The reasons for the poor diameter growth at Meunna were not immediately apparent. Parts of Meunna 266/1/2 had achieved crown closure resulting in increased competition and possible reduced

growth. Meunna 266/6 still retained the eucalypt nurse crop that would have had a negative impact on diameter growth in this trial. Apart from these two possible impacts on growth, no other likely causes of the slow growth at Meunna were apparent. Overall stem form was poor due to the lack of early form pruning to manage apical dominance and control branch growth.

Conclusion

Significant genetic variation in survival, growth and form were found across a number of mid-age blackwood progeny trials in northern Tasmania, Australia. This variation was partly explained by broad scale adaptive differences across the wide geographic distribution of blackwood. Seedlots from tropical Queensland origins had poor survival when grown in cool temperate Tasmania. At the regional level, local provenances were not necessarily the best performing. While there was significant genetic variation in the presence of single stemmed trees, the actual percentage of these single stemmed trees which had straight stems was low and not affected by seedlot origin, suggesting little genetic variation for this key trait. However significant genetic differences in trees with single stems and the number of large branches in the lower stem suggests that selection and breeding to improve these key traits is possible. Poor form means that blackwood requires intensive early form and lift pruning in order to produce high-value, appearance-grade sawlogs (eg. de Zwaan 1982; Nicholas *et al.* 1994a; Nicholas and Brown 2002; Medhurst *et al.* 2003). Nicholas and Brown (2002) recommended annual pruning over a 5- to 7-year period, with a final rotation length of 35-40 years. However they indicated that both height and diameter growth rates are compromised by form pruning, which is

expensive and accounts for 61% of total silvicultural costs (Nicholas and Brown 2002). With significant genetic variation in survival, growth and form there are opportunities to improve the commercial viability of blackwood plantations through genetic selection and breeding. Such improvements would help reduce the high silvicultural costs required to grow quality blackwood sawlogs.

Chapter 5: Quantifying Phenotypic Variation in Wood Colour in *Acacia melanoxylon*

Introduction

Australian blackwood (*Acacia melanoxylon* R.Br.) is a high-quality appearance-grade timber species with a 200-year history as a premium-grade furniture timber (Brown 2001). This species is one of the most widely distributed trees in eastern Australia growing over a latitudinal range from north Queensland (16°S) to southern Tasmania (43°S), and westwards into South Australia. Within Australia the timber has been sourced from native forest, with most of the current production coming from Tasmania (Jennings 1998; Featherston 2007; Forestry Tasmania 2008). Blackwood is also grown in plantations, including as an exotic in several other countries (Cowan and Maslin 2001). The timber is prized for its rich suite of colours, figured grain and workability. It is used in joinery, cabinetry, furniture, musical instruments and craft. Heartwood colour varies from pale cream, straw, golden-brown, red-brown and walnut-brown, with prominent annual growth rings. Sapwood is pale cream coloured (Boas 1947). This large colour range is associated with both between- and within-tree variation (de Zwaan 1982; Nicholas and Brown 2002). In few if any other woods can one find such a wide variety of natural colours (Harrison 1975a).

While sawn recovery appears to be a major driver in blackwood log pricing (Harington 2007), heartwood colour is also important (Nicholas 2007a). Wide between-

and within-tree wood colour variation is regarded as a problem particularly in markets where consistency is important (Lambert 2004; Nicholas 2007d). This variation provides challenges in terms of classifying blackwood wood products into both colour and colour variability classes to meet market requirements.

Three grades of blackwood dressed timber currently recognised in Australia focus on the presence/absence of features such as knots, straight grain and sapwood, and ignore heartwood colour variation (Tasmanian Timber Promotion Board 2006). Market research on blackwood has not extended to colour preferences (Lambert 2004; Nicholas 2007a; Nicholas 2007d) nor do the current Australian product standards include colour grading criteria (Standards Australia 1999; Standards Australia 2006a; Standards Australia 2006b). This absence of recognised colour and colour variation grades, and market-based pricing data relating to heartwood colour and colour variation, present impediments to the commercialization and breeding of blackwood as a plantation species. Developing an appropriate means of quantifying heartwood colour and colour variation together with appropriate economic weights for the colour traits would underpin an optimized tree breeding program for the species. Colorimetry is one technique that is increasingly being used to quantify wood colour.

A brief introduction and review of wood colour and of research in colour measurement using colorimetry was provided by Sullivan (1967b). Colorimetry has been applied to a variety of problems, particularly to changes in wood colour with different timber harvesting and processing techniques (Smith and Montoney 2000; Charrier *et al.* 2002; Mononen *et al.* 2002; Sundqvist 2002; Basri *et al.* 2003; Yeo and Smith 2003;

Rappold and Smith 2004). Fundamental research into relationships between wood colour and different wood sampling, sample preparation, measurement techniques and data analysis is scarce (Nelson *et al.* 1969; Hiller *et al.* 1972; Klumpers *et al.* 1993; Raymond and Bradley 2002; Hrčka 2008; Jung and Kozak 2008; Vanclay *et al.* 2008), with the result that development of standard methodologies in colour measurement, analysis and reporting remains an unresolved issue in wood science. One sampling issue is that of tree age and its affect on wood colour; one study found no effect in black walnut (*Juglans nigra*) (Nelson *et al.* 1969), while Klumpers *et al.* (1993) found a significant effect in oak (*Quercus petraea* and *Q. robur*), and Nelson and Heather (1972) found a significant effect of age on wood colour in *Eucalyptus grandis*.

A body of research has focused on between-species comparisons of wood colour (Sullivan 1967a; Nelson *et al.* 1969; Minemura *et al.* 1998; Nishino *et al.* 1998), and natural variation within species harvested from native forests (Klumpers *et al.* 1993; Burtin *et al.* 1998; Amusant *et al.* 2004; Bradbury 2005; Liu *et al.* 2005). Within-species wood colour variation includes between- and within-tree variation. There have been many reports into within-species and between-tree wood colour variation (Rink 1987; Mosedale *et al.* 1996; Raymond and Bradley 2002; Hannrup *et al.* 2004; Thulasidas *et al.* 2006; Bhat *et al.* 2007; Grekin 2007). Sotelo Montes *et al.* (2008) and Vanclay *et al.* (2008) represent the first comprehensive attempts to quantify the wood colour range and variation in timber species using extensive progeny material of *Calycophyllum spruceanum* in Peru, and *Eucalyptus dunnii* in Australia, respectively. Raymond and Bradley (2002) and Sotelo Montes *et al.* (2008) examined both between- and within-tree

colour variation. Within-tree colour variation is closely allied to patterns commonly caused by growth rings, but also by features such as knots, and tension and compression wood (Liu and Furuno 2002; Lu and Tan 2004; Kibblewhite *et al.* 2005). Jung and Kozak (2008) provided valuable fundamental research evaluating the effects on wood colour using eight different colorimetric standard illuminant sources, while Hrčka (2008) provided a mathematical approach to defining wood colour for individual species. The use of different illuminant and observer standards in colorimetry results in different colour measurements being recorded.

The accurate and repeatable measurement of colour requires understanding and controlling three elements: a) the object to be measured, b) the light source and c) the observer standard. The International Commission on Illumination (CIE) has set colorimetric standards for the correct measurement of colour using a range of light source (illuminant) and observer standards (Wyszecki and Stiles 1982). Each of these illuminants can produce significantly different results (Jung and Kozak 2008). The measurements can then be expressed in a range of colour scales or spaces. While there are several colour spaces that have historically been used in wood colorimetry (Sullivan 1967a; Nelson *et al.* 1969; Rink 1987; Wilkins and Stamp 1990), the most common currently used is the CIELAB (Nishino *et al.* 1998; Janin *et al.* 2001; Raymond and Bradley 2002; Hannrup *et al.* 2004; Bradbury 2005; Liu *et al.* 2005; Kokutse *et al.* 2006; Grekin 2007; Nicholas *et al.* 2007; Sotelo Montes *et al.* 2008; Vanclay *et al.* 2008). This is the most complete colour space specified by the CIE for use in colorimetry. It describes all the colours visible to the human eye and was created to serve as a device-

independent model to be used as a reference. The three coordinates of CIELAB represent the lightness of the colour (L*), its position between red and green (a* = redness) and its position between yellow and blue (b* = yellowness). The nonlinear relations for *L**, *a**, and *b** are intended to mimic the nonlinear response of the human eye. Furthermore, uniform changes of components in the colour space aim to correspond to uniform changes in perceived colour, so the relative perceptual differences between any two colours can be approximated by treating each colour as a point in a three dimensional space and taking the Euclidean distance between them (ΔE76) (Wyszecki and Stiles 1982).

Six previous studies have investigated blackwood heartwood colour in relation to genetics (Nicholas *et al.* 1994b), site and silvicultural effects (Harrison 1975a; Harrison 1975b; Bradbury 2005; Nicholas *et al.* 2007), and pulping properties (Lourenço *et al.* 2008). Harrison (1975b; 1975a) assessed heartwood colour, and between- and within-tree colour variation using a unique visual grading system. Nicholas *et al.* (1994b; 2007) used a simple visual colour rating system, and together with Bradbury (2005) and Lourenço *et al.* (2008) used colorimetry and the CIELAB colour space. Differences in methodology and lack of full reporting of methods in these past studies preclude any direct comparison with the current study.

Wood colour variation and consistency are recognised as significant issues in blackwood markets. The present study uses colorimetry to measure the range and within- and between-tree colour variation in a selection of blackwood progeny trial material from Tasmania. The objectives were to 1) define the blackwood sapwood and heartwood

colour spaces, 2) measure between- and within-tree heartwood colour variation using colorimetry, and 3) determine which attributes of the quantified colour space best reflect variation as determined by subjective classification of commercially significant colour and colour variation. This forms part of a larger study aimed at addressing the genetic and environmental variation in blackwood wood properties, including heartwood colour.

Materials and Methods

Core samples

Twelve-mm diameter stem cores were collected from twelve trees representing each of 16 open-pollinated single-tree families, originating from across Tasmania, which were growing in three 19 year-old blackwood progeny trials in northern Tasmania. This sample of trials and families were selected as it was the largest balanced sample of families available, based on a survey of blackwood genetic resources (Chapter 2), and subsequent assessment of five trials for survival, growth and form (Chapter 4). The family samples at each site were distributed across two-to-three replicates. One trial was located at Meunna (41° 05'S, 145° 28'E), while two were located at Virginstow (41° 18'S, 146° 36'E) (Allen 1992). The stem cores were randomly selected from 12 trees per family within each replicate and taken at breast height (1.3 m) in a north-south direction, with no cores taken from trees with a diameter at breast height of < 10 cm. Cores were labelled and wrapped in plastic film before being refrigerated. Following oven drying at 105°C the cores were mounted into routed dressed boards of *Pinus radiata* using polyvinyl acetate (PVA) glue. The boards were then put through a commercial machine

sander to remove half of each core and expose a dressed radial core surface suitable for colour measurement.

Colour measurement

Colour measurements were taken on the dressed cores soon after sanding to minimise changes in colour from oxidation and photo-chemical effects. The boards containing the cores were kept covered in black plastic when not being measured. Colour was

measured using a Minolta CR400 Chroma Meter. This instrument has an 8 mm diameter measuring aperture, and allows the choice of one (2°) observer standard, and either of two illuminant standards (C and D65). Colour data were recorded using the C illuminant and the CIELAB colour space (Wyszecki and Stiles 1982). Colour measurements of the heartwood were taken in 8 mm radial increments from the pith to the visible heartwood-sapwood boundary on either side of the pith, with care to avoid including sapwood in the colour data. This resulted in a variable number of heartwood colour measurements per core depending upon the length of the core and the amount of heartwood within each core. Two single sapwood colour measurements were taken from each core, one either side of the pith centred between the heartwood-sapwood boundary and the outer edge of the core under bark (Figure 5.1).

Core classification

Cores were visually sorted into four classes for both heartwood colour (1-4) and heartwood colour variability (1-4), where 1 was very good and 4 was very poor. The classification was entirely subjective in the absence of market-related data. Colour

Figure 5.1: Measuring the colour of blackwood stem cores mounted into pine boards.

classification was mostly based on lightness, with colour class 1 containing red-brown and walnut-coloured cores, while class 4 contained pale straw-coloured cores. Visual assessment of colour variability was more difficult. In addition to blackwood's prominent annual growth rings some colour variability is expected in most blackwood markets. This richness of colour is an important feature of blackwood. However too much or too little colour variability, or colour variability that produces an irregular pattern, may be less marketable. Therefore variability class 1 contains samples with regularly patterned moderate colour variation, while class 4 contains samples with irregular, very high or very low colour variation. Variability classes 2 and 3 represent intermediate positions between classes 1 and 4. This classification provided a context for analysing and discussing blackwood colour, and provided a framework within which to determine which colorimetric measures and derived values were best associated with perceived colour and colour variability differences.

Data analysis

Heartwood and sapwood colour ranges were quantified by 1) the absolute values and ranges of each of the three CIELAB axes, and 2) the calculated difference (ΔE76) between the mean CIELAB lightness (L*), redness (a*) and yellowness (b*) values and each colour measurement. Delta E ($\Delta E76 = \sqrt{\Delta L^2 + \Delta a^2 + \Delta b^2}$) is a measure of colour difference, namely the Euclidean distance between two colours measured in the CIELAB colour space. A ΔE76 of 1.0 is the smallest colour difference perceptible to the human eye. Pearsons correlations between the three colour axes for both heartwood and

sapwood, and between heartwood and sapwood means, were calculated using SAS ProcCorr (ver. 9.1, SAS Institute Inc. 2004) based on all data and core means.

To measure within-tree colour variation, differences (ΔE76) were calculated between all heartwood colour measurements, and between the two sapwood measurements, within each core. Core mean ΔE76 values were then calculated for heartwood and sapwood, and maximum ΔE76 values calculated for heartwood. Within-tree colour differences (ΔE76) between heartwood and sapwood colour were calculated using the mean ΔE76 values. To calculate between-tree colour variability, differences (ΔE76) were calculated between mean heartwood and sapwood colour measurements.

A one-way analysis of variance based on core means was fitted using Proc MIXED of SAS to test which colorimetric parameters relate to the visual colour and colour variability classes. When a significant effect was detected within the mixed model analyses, the Tukey-Kramer test for multiple comparisons was used to determine which classes were significantly ($p < 0.05$) different.

Results

Heartwood and sapwood colour

Across all data heartwood had an overall lightness (L*) mean of 62.5 with values from 37.3 to 88.8 and a range of 51.5, which is over half of the total lightness range of 0 to 100. The lightness range based on core means was 33.6. Redness (a*) overall mean was 9.5 with values from 1.2 to 15.3. Yellowness (b*) overall mean was 20.4 with values from 10.3 to 26.7. Sapwood had overall lightness (L*) values from 60.7 up to a very

bright 91.1 with a mean of 82.2, and redness (a*) values as low as 1.2 (Table 5.1). Heartwood and sapwood values within the CIELAB colour space adjoin and partly overlap (Figure 5.2). Heartwood colour values were comparable with those from other blackwood studies where the use of dry wood samples and the CIELAB colour space allowed some degree of comparison (Table 5.2).

Table 5.1: Summary statistics for all data and core means for heartwood and sapwood colour

	Colour Trait [1,2]	n	Mean	SD	Min	Max
		All data				
Heartwood	L*	6650	62.5	5.8	37.3	88.8
	a*	6650	9.5	1.7	1.2	15.3
	b*	6650	20.4	1.7	10.3	26.7
	ΔE76	6650	5.3	3.4	0.2	27.8
Sapwood	L*	1310	82.2	4.0	60.7	91.1
	a*	1310	3.0	1.2	0.3	8.5
	b*	1310	15.2	1.8	10.2	23.1
	ΔE76	1310	3.8	2.4	0.3	22.2
		Core means				
Heartwood	L*	567	62.7	4.8	51.4	85.1
	a*	567	9.5	1.4	2.7	13.8
	b*	567	20.3	1.2	15.3	24.3
	ΔE76	567	4.5	2.8	0.1	23.7
Sapwood	L*	572	82.2	3.5	68.1	90.0
	a*	572	3.0	1.1	0.5	6.1
	b*	572	15.2	1.4	11.1	20.9
	ΔE76	572	3.4	2.0	0.2	14.7

Notes:

1. Colour represented in the CIELAB colour space where L* represents lightness (0 - black, 100 - white), a* represents redness (green (-ve) to red (+ve)), and b* represents yellowness (blue (-ve) to yellow (+ve)).
2. Delta E (ΔE76) is a measure of difference (or distance) between colours. In the above table it is the distance from the mean Lab values.

Table 5.2: Comparison of current blackwood colour values with results from previous studies

Study details	Colour Trait	Mean	SD	Min	Max
Nicholas *et al.* (1994) [a]	L*	39.1 - 45.4		16.0 - 33.4	49.8 - 58.1
Heartwood	a*	7.9 - 8.6		3.0 - 6.1	10.0 - 14.7
	b*	23.0 - 24.8		4.9 - 18.3	30.0 - 38.8
Bradbury (2005) [b]	L*	57.2 - 62.0			
Heartwood	a*	10.0 - 11.8			
	b*	19.4 - 21.5			
Nicholas *et al.* (2007) [c]	L*	58.7	3.5	46.9	67.4
Heartwood	a*	9.1	1.5	6.0	14.0
	b*	18.8	1.4	15.3	22.5
Lourenço *et al.* (2008) [d]	L*	55.0		50	62
Heartwood	a*	11.3		9	13
	b*	22.4		21	23
Sapwood	L*	77.0		71	82
	a*	4.8		4	6
	b*	20.4		19	23
Current study	L*	62.5	5.8	37.3	88.8
Heartwood	a*	9.5	1.7	1.2	15.3
	b*	20.4	1.7	10.3	26.7
Sapwood	L*	82.2	4.0	60.7	91.1
	a*	3.0	1.2	0.3	8.5
	b*	15.2	1.8	10.2	23.1

Notes:

a. Nicholas *et al.* (1994) involved stem disc sampling from 59 trees of 10 yr-old, progeny trial material, four seedlots, green wood samples, with colour measured on rough sawn transverse surfaces, 4 measurements per disc. The mean range of values relate to seedlot means.

b. Bradbury (2005) involved stem core sampling from 210 trees aged 14-22 yr-old native forest regeneration and one family seedlot from a progeny trial, oven-dried samples, with colour measured on dressed radial surfaces, 2 measurements per core. The range of values relates to sample unit (forest harvest area) means.

c. Nicholas *et al.* (2007) involved stem disc sampling from 306 trees of 18 yr-old, silvicultural trial material, one seedlot, oven-dried samples, with colour measured on rough-sawn transverse surfaces. Overall means are shown.

d. Lourenço *et al.* (2008) involved measuring colour of 20–40 mesh wood flour samples, from discs of 20 trees collected across four sites in Portugal, with ages ranging from 28–43 years. The minimum and maximum values were read from Fig. 2 in the article.

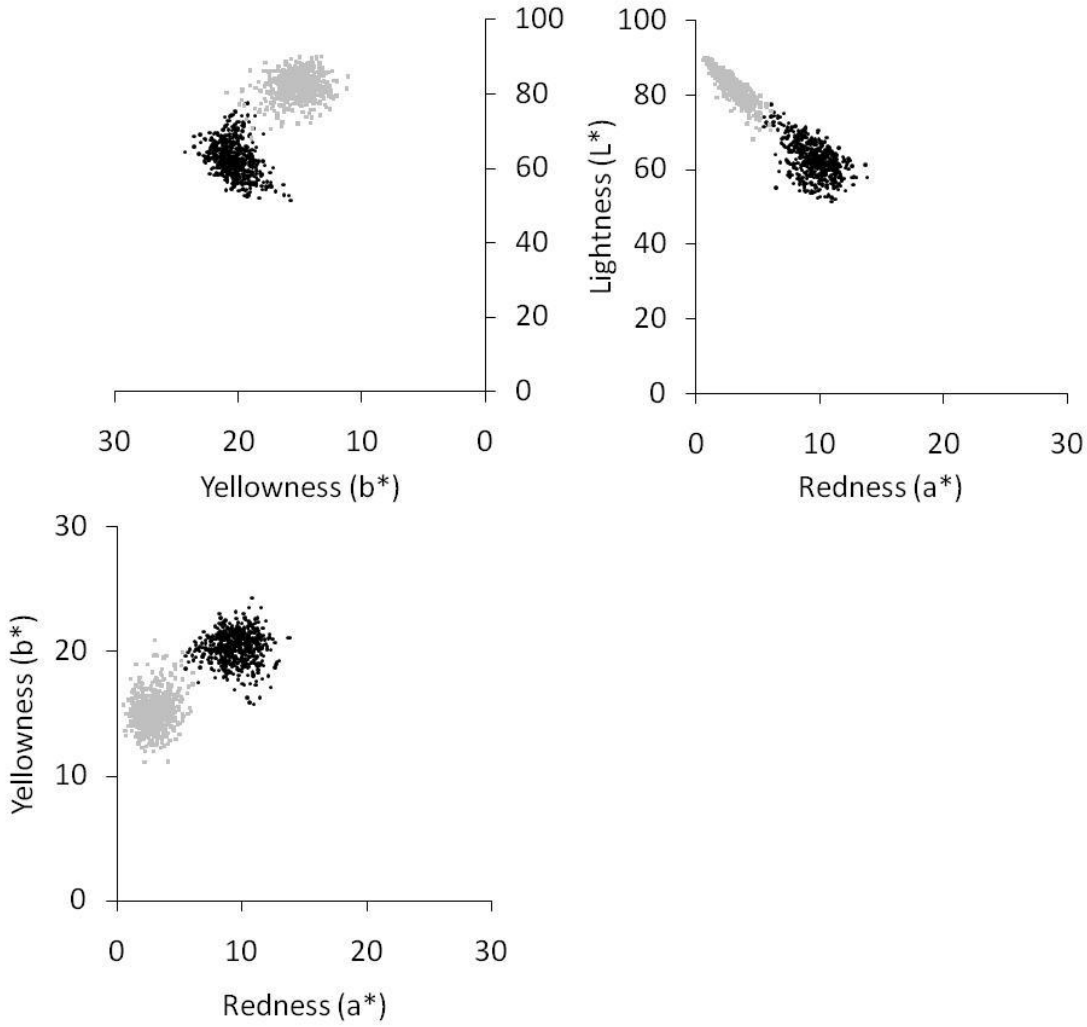


Figure 5.2: The blackwood heartwood (•) and sapwood (•) colours represented in the CIELAB colour space, viewed in each of the three planes. L* represents lightness (0 - black, 100 - white), a* represents redness (green (-ve) to red (+ve)), and b* represents yellowness (blue (-ve) to yellow (+ve))

Correlations amongst colour axes for both heartwood and sapwood were moderate to low, except between sapwood lightness (L*) and redness (a*) across core means (r = -0.86, p < 0.0001), and across all data (r = -0.83, p < 0.0001) (Table 5.3). Colour variation in the sapwood space is consequently not independent, with increasing lightness being associated with decreasing redness. Correlations between within-tree

Table 5.3: Pearsons correlations (r) and their significance for heartwood and sapwood colour axes across all data (above)[2,3] and core means (below)[2,3]

	Lightness (L*)	Redness (a*)	Yellowness (b*)
		Heartwood	
Lightness (L*)		-0.55***	0.39***
Redness (a*)	-0.55***		0.03*
Yellowness (b*)	0.31***	0.07	
		Sapwood	
Lightness (L*)		-0.83***	-0.22***
Redness (a*)	-0.86***		0.29***
Yellowness (b*)	-0.17***	0.16**	

Notes:
1. Significant correlations * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$.
2. Above diagonal all data, below diagonal core mean data
3. Heartwood n = 6650 all data, n = 567 core means; sapwood n = 1310 all data, n = 572 core means

sapwood and heartwood colour were moderate to low, with the strongest correlations between heartwood and sapwood lightness ($r = 0.39$, $p < 0.0001$), and heartwood redness and sapwood lightness ($r = -0.41$, $p < 0.0001$) and redness ($r = 0.40$, $p < 0.0001$) (Table 5.4), precluding the possibility that heartwood colour in standing trees could be determined by measuring sapwood colour.

Table 5.4: Pearsons correlations (r) between heartwood and sapwood colour based on core means (n = 567). Significant correlations * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$

		Heartwood	
Sapwood	Lightness (L*)	Redness (a*)	Yellowness (b*)
Lightness (L*)	0.39***	-0.41***	-0.10*
Redness (a*)	-0.28***	0.40***	0.18***
Yellowness (b*)	-0.20***	0.09*	-0.17***

Colour variation

Blackwood heartwood colour exhibited high levels of between- (mean ΔE76 = 5.4) and within- (mean ΔE76 = 4.5) tree variation, within the genetic material sampled. Between- and within- tree sapwood colour variability was less than that for heartwood (Table 5.5).

Table 5.5: Within- and between-tree heartwood and sapwood colour variation (ΔE76)

	Mean	SD	Min	Max
Mean difference in heartwood colour within cores	4.5	1.6	1.1	14.0
Maximum difference in heartwood colour within cores	10.9	4.7	1.9	32.2
Mean difference in sapwood colour within cores	3.7	2.7	0.3	21.6
Difference between mean heartwood and sapwood colours within cores	21.4	4.4	1.5	33.6
Difference in mean heartwood colour between trees	5.4	3.8	0.3	32.2
Difference in mean sapwood colour between trees	4.0	2.7	0.2	16.4

Heartwood classification

Both mean lightness (L*, $p < .0001$) and mean redness (a*, $p < .0001$) were highly significantly different between the visual heartwood colour classes. Mean lightness decreased while mean redness increased with increasing acceptability. The Tukey-Kramer test showed significant separation between all four classes with these colour traits ($p < 0.05$). Both mean ($p < 0.0001$) and maximum ($p < 0 .0001$) within-tree heartwood ΔE76 were highly significantly different between the visual heartwood colour

variability classes. There was no significant association between the mean within-tree heartwood colour variation and the visual colour classes (Table 5.6).

Table 5.6: Summary data and mixed model analysis results for visual heartwood colour and colour variability classification. Levels of significance for F values are *** = p < 0.001, ** = p <0.01. Values in the row followed by the same letter do not differ significantly based on Tukey-Kramer adjustment for multiple comparisons (*p* < 0.05)

	$F_{3,562}$	Very Good (1)	Good (2)	Poor (3)	Very Poor (4)
Colour Class (n)		282	115	109	60
Mean lightness (L*)	209.3***	60a	62.4b	65.7c	70.4d
Mean redness (a*)	71.1***	10.1a	9.6b	9c	7.7d
Mean yellowness (b*)	7.5***	20.1a	20.5b	20.7b	20.5ab
Mean of Maximum ΔE76	6.4***	11a	11.2a	10.9a	8.8
Colour Variability Class (n)		161	168	142	95
Mean ΔE76	16.6***	3.9a	4.3ab	4.7b	5.3c
Maximum ΔE76	61.3***	8.7a	9.6a	11.8b	15.7c

Discussion

This study provided the first major colorimetric analysis of blackwood wood colour and colour variation, albeit on a limited range of families from Tasmania. It demonstrated that both blackwood heartwood and sapwood have large colour ranges. Mean heartwood lightness (L*) was slightly higher (lighter coloured) than that reported by Bradbury (2005) and Nicholas *et al.* (2007), while mean redness (a*) and yellowness (b*) were similar. Neither of these authors reported the colorimetric standards used in their studies preventing direct comparison of results. The overall range of heartwood lightness (L*), yellowness (a*) and redness (b*) values, however, was much larger. Blackwood

heartwood colour range as measured by standard deviation for the three colour coordinates recorded by Nicholas *et al.* (2007) from dried rough-sawn end-grain were comparable with core mean standard deviations found in this study. However the use of rough-sawn surfaces for colour measurement has been questioned by Vanclay *et al.* (2008). Using 9 year-old *E. dunnii* progeny trial material, they found that correlations between colour measurements of sanded and rough-sawn material were low, with sanding necessary for reliable measurements. Whether this finding also applies to end grain and other wood surfaces, and to other species, remains unknown.

Raymond and Bradley (2002) found strong regression relationships between green and air-dried rough-sawn transverse surfaces of *Eucalyptus nitens* for lightness (L*, r^2 = 0.72) and redness (a*, r^2 = 0.62), with a weaker relationship for yellowness (b*, r^2 = 0.55). If the blackwood heartwood colour values from green discs by Nicholas *et al.* (1994b) are compared with the oven-dried samples of this and other studies, lightness (L*) values were much lower (darker), redness (a*) values were comparable, while yellowness (b*) values occupied a much wider range, with lower (more blue) minimum yellowness values. These comparisons are similar to those of Raymond and Bradley (2002). Further research on the relationships between the colour of green and dried, and rough-sawn and dressed wood samples is warranted to help standardize wood colour measurement techniques, and help determine whether non-destructive, in-field colorimetric assessment of wood colour can be made with confidence. For example Dudley and Yamasaki (2000) found branch heartwood colour could be used to accurately predict stem heartwood colour in dressed, dried samples of *Acacia koa* in Hawaii.

When colour spaces are defined as the distance from the mean CIELAB values (ΔE76), sapwood mean ΔE76 (3.8) was smaller than the heartwood mean ΔE76 (5.3) colour space. Only a few authors have used the distance from the mean CIELAB values to define a species colour range. Vanclay *et al.* (2008) found a mean ΔE76 of 8.4 from a "typical" heartwood sample of *E. dunnii*, from dried rough-sawn radial surfaces. This suggests a much larger colour range for *E. dunnii* than for blackwood, although their finding that rough-sawn surfaces did not give reliable colour measurements may be relevant to this result. Hrčka (2008) found maximum ΔE76 from mean CIELAB values for European spruce (*Picea abies* L.) and beech (*Fagus sylvatica* L.) of 1.7 and 13.3 respectively; most of the beech observations were ≤ 3.9 which is comparable with blackwood sapwood and much less than blackwood heartwood. The greater beech colour distance values reflected the presence of discoloration.

The D65 illuminant and 10° observer colorimetry standards were used to make multiple colour measurements on dried tangential surfaces of heartwood samples from a 39-month-old progeny trial of *C. spruceanum* containing 200 open-pollinated families across seven provenances planted at two sites (Sotelo Montes *et al.* 2008). They found colour ranges of 19.4, 7.7 and 7.7 for lightness (L*), redness (a*) and yellowness (b*) respectively across all data. This colour range is less than half that of blackwood heartwood or sapwood found in this study. Ranges of 32.1, 12.5 and 14.9 for lightness (L*), redness (a*) and yellowness (b*) respectively were recorded from multiple measurements on dried, planed radial surfaces of European beech (*Fagus sylvestris*)

heartwood samples from 83 trees located in nine natural stands (Liu *et al.* 2005), which compares with the colour range of blackwood sapwood.

Blackwood sapwood appeared to be a remarkably light coloured timber with lightness values up to 91.1 and very low redness values (overall mean of 3.0). Blackwood sapwood is generally used in wall paneling in the Black and White Grade (Tasmanian Timber Promotion Board 2006), where the contrast between dark heartwood and the light sapwood creates a dramatic visual effect. Within-tree differences between mean heartwood and sapwood colour (ΔE76) varied widely from 1.5 to 33.6, with a mean of 21.4. These differences would therefore affect the quality of the Black and White Grade as small differences in colour between heartwood and sapwood would result in less visual contrast. Colorimetry could be used to determine a minimum standard for ΔE76 between sapwood and heartwood that could be used as an objective measure with the current Black and White Grade.

There are few studies of sapwood colour (Boardman *et al.* 1992; Mosedale *et al.* 1996; Burtin *et al.* 1998; Nishino *et al.* 2000; Charrier *et al.* 2002; Mononen *et al.* 2002; Vanclay *et al.* 2008), and fewer reporting sapwood colour range (Burtin *et al.* 1998; Mononen *et al.* 2002). Burtin *et al.* (1998) examined the wood colouring process from sapwood to heartwood and its relationship to extractives in three species of oak. Multiple colour measurements were made on freeze-dried and sanded radial surfaces. Mean and standard deviations for lightness (L) for inner and outer sapwood ranged from 84.2±1.09 to 87.9±0.51 (Burtin *et al.* 1998). These standard deviations are low compared to those for blackwood sapwood lightness (3.5 for core means). Mononen *et al.* (2002)

investigated the effects of felling season and log storage on heartwood and sapwood colour of native forest silver birch (*Betula pendula*) in Finland. They found mean sapwood lightness (L*) values of 62.5 to 70.7, redness (a*) values of 4.1 to 5.7 and yellowness (b*) values of 11.5 to 14.2. This range of values was also much less than for blackwood sapwood.

In light coloured silver birch, ΔE76 of 5 to 10 were rated as great; values >10 were rated very great (Mononen *et al.* 2002). If visual perceptions of colour difference for dark-coloured timbers like blackwood are like those for light coloured timbers, then the mean between-tree colour difference in silver birch was similar as mean and maximum within-tree ΔE76 for blackwood in this study were 4.5 and 10.9 respectively. Significant differences in blackwood heartwood colour were also found vertically within trees across plantations in South Africa (Harrison 1975a; 1975b), with lightness increasing and red and brown pigments decreasing with increasing height. Within-tree colour variation differed significantly between regions of the country, but not within regions. These high levels of between- and within-tree colour variability are a concern in terms of colour consistency, with further research required to determine the colour tolerances acceptable to the various sectors of the blackwood industry.

High within-tree colour variation may not be a problem for end-users of timber, provided the variability is expressed as a regular pattern, and there is sufficient quantity of consistent colour and colour variability to meet market demand. With the exception of luthier timber most blackwood is back or crown sawn to highlight the distinctive annual growth rings and colour patterns. However blackwood can also exhibit irregular colour

patterns, such as dark coloured bands of tension wood (Hillis *et al.* 2004) that may present problems for some users, but can be a valuable feature for users such as luthiers. Where surveys have shown that consistency of colour are a major market requirement, of the actual wood itself appears to be of less importance (Lambert 2004).

In a comparable study into within-tree colour variation, *C. spruceanum* had a mean sum of within-tree ΔE76 across all data of 13.7. Each wood sample had eight colour measurements with colour differences being calculated only between adjacent measurements and hence seven colour difference measurements were calculated. This gave a mean ΔE76 of 1.96 (ie. 13.7/7), and minimum and maximum variation of 0.7 to 4.9 (Sotelo Montes *et al.* 2008). These results are not strictly comparable with the blackwood results from this study where colour differences were calculated between all measurements within each core sample. However this comparison indicates that blackwood heartwood has potentially greater within-tree variability than *C. spruceanum.* Moslemi (1967) in a report on quantitative colour measurement in black walnut heartwood found ΔE76 between one veneer sample selected as a reference, and 23 others of 3.2 to 11.6 with a mean of 6.9; these differences are comparable with within-tree mean differences in blackwood heartwood.

The matching of visual colour and colour variability grades against colorimetric data indicates that colorimetry can potentially be used to quantify these subjectively determined grades. An alternative approach would be to dissect the known heartwood colour space into grades that are then verified as meaningful to the market. This potentially avoids the problem where visual colour grades overlap to such an extent that

their separation using colorimetry becomes difficult (Boardman *et al.* 1992). The problem of colour overlap in visual product grades in black walnut veneer (Boardman *et al.* 1992) may have been due to within-tree and within-grade colour variation not being properly accounted for. Where wide between and within-tree colour variation is found such as in blackwood heartwood, colour grading must account for both. Nevertheless automated colorimetric techniques have been successfully used to grade solid wood for defects or colour (Vienonen *et al.* 2002).

Conclusion

While based on a limited range of genetic material from Tasmania, this study was the first to quantify the within- and between- tree wood colour variation in Australian blackwood. Blackwood heartwood and sapwood have wide colour ranges, with wide within- and between- tree colour variation, while colour and colour consistency are recognised as important to the blackwood processing industry. Both issues provide an incentive to develop industry-standard product grades for heartwood colour and colour variation using colorimetry to better meet the needs of blackwood markets. To develop product grades, research is needed to identify market preferences for blackwood colour and colour variation, with at least relative pricing indices for the colour grades. This would also assist the domestication of blackwood as a plantation species, where heartwood colour should be included, along with other wood properties, as a trait in selection and breeding programs. Changes in colour preferences over time with fashion would be reflected in changing demand for different colour grades, and become one of the risk factors in domestication and breeding. This study demonstrated that colorimetry

can be used to quantify the wide colour variation in blackwood, and help define visually graded core samples. Research into the effects of tree age on heartwood colour in blackwood is warranted to ensure that product colour grades reflect heartwood colour in mature trees.

Chapter 6: Genetic and Environmental Variation in Heartwood Colour of *Acacia melanoxylon*

Introduction

Australian blackwood (*Acacia melanoxylon* R.Br.) is a premium appearance-grade timber used in stringed musical instruments, furniture, cabinetry and craft; with heartwood colour varying from pale cream, straw, golden-brown, red-brown and walnut, with prominent dark annual growth rings (Bootle 2005). This colour range is expressed as both between- and within-tree variation, and is regarded as a problem in markets for appearance-grade timber where colour consistency is important (Lambert 2004; Nicholas 2007d). Within- and between-tree heartwood colour variation also presents challenges in the domestication of blackwood as a commercial plantation species, as the extent of the variation and the genetic and environmental control remains unknown.

The CIELAB colour space is an international standard for recording colour. It is widely used to record wood colour (Amusant *et al.* 2004; Kokutse *et al.* 2006; Hrčka 2008; Moya and Berrocal 2010). In this space colour is recorded in a three-dimensional coordinate system, where L* (lightness) records the black-white value (0 – 100), a* (redness) records the green (-ve) to red (+ve) value, and b* (yellowness) records the blue (-ve) to yellow (+ve) value. The CIELAB colour space allows the calculation of colour difference or change (ΔE76), such that a ΔE76 of 1.0 is the smallest change in colour that the human eye can perceive (Wyszecki and Stiles 1982).

Blackwood heartwood colour has previously been investigated in relation to genetics (Nicholas *et al.* 1994b) and site and silvicultural effects (Harrison 1975b; Harrison 1975a; Bradbury 2005; Nicholas *et al.* 2007). Significant differences in colour and within-tree colour variation were found between regions, but not within regions, in blackwood plantations in South Africa (Harrison 1975b). High rainfall and number of rain-days were associated with darker colour, while increasing brownness and within-tree colour uniformity were associated with a well-defined cold-induced dormant period. Significant within-tree variation in heartwood colour was also found, with increasing lightness and decreasing redness and brownness being positively associated with height in the stem (Harrison 1975a).

No significant difference in heartwood colour was found between four 10-year-old blackwood seedlots in New Zealand but extreme between-tree heartwood colour variation was found in three of the four seedlots (Nicholas *et al.* 1994b). In a second study, Nicholas *et al.* (2007) found significant differences in redness (a*) and yellowness (b*) but not lightness (L*), between five sites in a silvicultural trial containing a single blackwood provenance. In Tasmania no significant difference in heartwood colour was found between two silvicultural regimes in native blackwood regrowth or a single open-pollinated family from a progeny trial (Bradbury 2005).

There have been few studies of the genetic and environmental variation in wood colour in any tree species. Significant environmental effects on heartwood colour have been found for black walnut (*Juglans nigra*) (Rink 1987), European oak (*Quercus petraea and Q. Robur*) (Mosedale *et al.* 1996) and *Calycophyllum spruceanum* (Sotelo

Montes *et al.* 2008): significant genetic effects were found for European oak (Mosedale *et al.* 1996), *C. spruceanum* (Sotelo Montes *et al.* 2008) and *Eucalyptus dunnii* (Vanclay *et al.* 2008); significant environmental by genetic interaction effects have been found for 21- 38 year-old European oak (Mosedale *et al.* 1996), but not for within-tree heartwood colour variation in *C. spruceanum* at age 39 months (Sotelo Montes *et al.* 2008).

A companion chapter examined the extent of phenotypic variation in the same stem core samples (Chapter 5). This previous study found moderate but significant phenotypic correlations between blackwood heartwood lightness (L*) and redness (a*: r = -0.55, p<.0001) and lightness and yellowness (b*: r = 0.39, p<.0001), indicating that decreasing lightness is correlated with increasing redness and decreasing yellowness. The objective of this study was to determine the extent of genetic and environmental variation in between- and within-tree heartwood colour variation in blackwood.

Material and Methods

Trials & Genetic Material

Sixteen open pollinated families were common across three blackwood progeny trials in northern Tasmania, all established in 1989. One trial was located at Meunna (266/2/2), while two were located at Virginstow (266/4/1 and 266/4/2) (Allen 1992). The trials were of random complete replicate design. Meunna 266/2/2 and Virginstow 266/4/2 were pure blackwood plantings with families represented as family line plots of 20 trees in each replicate, with spacing of 3.0 m between rows and 4.2 m within rows. The other trial Virginstow 266/4/1 involved plantings of the same blackwood families in two

replicates but with a nurse crop of one of the main plantation eucalypts grown in this area, *Eucalyptus globulus.* In this case, family plots were of approximately 0.2 ha in area (3.0 m spacing between and 4.2 m within rows for the blackwood and 2.1 m within rows for the eucalypt), comprising alternate rows of the single blackwood family and *E. globulus*, with a minimum of seven rows of blackwood per plot. The nurse crop was included as it was expected to enhance blackwood survival and form. Meunna has deep, fertile, kraznozem soils, high rainfall (1600 mm yr^{-1}) and is at an altitude of 320 m and can be regarded as a good site for growth of blackwood. Virginstow has poor soils and lower rainfall (930 mm yr^{-1}), is at an altitude of 160 m and can be regarded as a poor blackwood site. The Virginstow trials were spatially intermixed with planting bays of the nurse crop trial alternated with planting bays of the pure blackwood trial None of the trials had received any thinning or pruning.

Seeds of the families in the trials were collected from around Tasmania in 1988 from trees of superior form (Neilsen and Brown 1996). The 16 families selected for the current study formed the largest available sample of families tested across multiple trial sites, based on a survey of blackwood trials (Chapter 2), and subsequent assessment of five trials for survival, growth and form (Chapter 4). Twelve-millimetre stem cores were collected from 12 trees across two-to-three replicates per family in each trial, from trees randomly selected within each replicate. Trres were 19 years-old when sampled. Cores were taken at breast height (1.3 m) in a north-south direction, with no cores taken from trees with a stem diameter at breast height of less than 10 cm. Cores were labelled and wrapped in plastic film before being refrigerated. The cores were oven-dried at 105°C

and mounted into routed channels on boards of clear *Pinus radiata* using polyvinyl acetate (PVA) glue. The boards were then put through a commercial sander to remove half of each core and expose a dressed radial face suitable for colour measurement.

Colour measurements

Colour measurements were taken on the bare dressed cores soon after the cores were sanded to minimise changes in colour from oxidation and photo-chemical effects. No finishing oil or vanish was applied to enhance the wood colour. The boards containing the cores were kept covered in black plastic when not being measured. Colour was measured using a Minolta CR400 Chroma Meter. This instrument has an 8-mm diameter measuring aperture. Colour measurements of the heartwood were taken in 8-mm radial increments from the pith to the visible heartwood-sapwood boundary on either side of the pith, with care to avoid the inclusion of sapwood in the colour data. Two single sapwood colour measurements were taken from each core, one on each end of the core. Colour data were recorded using the three-dimensional CIELAB colour space (Wyszecki and Stiles 1982) using the C illuminant, and the 2° observer standards.

Data analysis

The data were analysed statistically using a mixed model, with within-tree colour variation modelled using a three-knot cubic spline (Verbyla *et al.* 1999; White *et al.* 1999) using ASREML (Gilmour *et al.* 2006). Splines are a flexible class of curves used to model complex shapes. The cubic spline was included to test for non-linear patterns of within-tree radial colour variation. As the number of heartwood colour measurements per core varied with core length and proportion of heartwood, each colour measurement

position was converted to a percentage distance (DIST) from the pith to the sapwood/heartwood boundary. The model fitted was:

Equation 6.1: Y = TRIAL + FAMILY + DIST + TRIAL.FAMILY + DIST.TRIAL + DIST.FAMILY + DIST.FAMILY.TRIAL + *TREE* + *SPLINEDIST* + *SPLINEDIST.TRIAL* + *SPLINEDIST.FAMILY* + *SPLINEDIST.FAMILY.TRIAL* + *DIST.TREE* + *SPLINEDIST.TREE* + *RESIDUAL*

where Y is a vector of observations; TRIAL and FAMILY are the trial and family effects respectively, both fitted as fixed factors; DIST is the proportional distance from the pith to the sapwood/heartwood boundary fitted as a covariate; TRIAL.FAMILY, DIST.TRIAL, DIST.FAMILY and DIST.FAMILY.TRIAL are the corresponding trial by family, distance by trial, distance by family and distance by family by trial interactions; *TREE* is the tree within trial and family effect, fitted as a random factor; *SPLINEDIST* is a random cubic spline component corresponding with the DIST term; *SPLINEDIST.TRIAL*, *SPLINEDIST.FAMILY*, *SPLINEDIST.FAMILY.TRIAL*, *DIST.TREE* and *SPLINEDIST.TREE* are the random-spline by trial, random-spline by family, random-spline by family by trial, proportional distance by tree and random-spline by tree interactive effects respectively, fitted as random factor-covariate/spline interactions; and *RESIDUAL* is a random vector of residuals. The significance of random terms in the model was calculated using a Z-test, whereas the significance of the fixed effects and covariate was tested using an F-test, with random between-tree variation used

to test trial, family and their interaction and other terms associated with within-tree variation (DIST) tested with the overall model residual.

Results and Discussion

Between-tree wood colour variation

Significant genetic (i.e. family), environmental (i.e. trial), and genetic-by-environment interaction effects on tree mean heartwood lightness (L*), redness (a*) and yellowness (b*) were found; there was significant random variation between trees within families at each trial (TREE) for all three colour traits (Table 6.1). The trial effect was due to the significantly greater mean lightness (L*) and lower mean redness (a*) and yellowness of trees in Virginstow 266/4/1, while there was no significant difference between Meunna 266/2/2 and Virginstow 266/4/2 in tree mean colour (Figure 6.1). Harrison (1975a) suggested higher rainfall, more rain-days, and a cold-induced dormancy as necessary to produce darker, more uniform coloured blackwood. These factors did not explain the colour variation between trials in this study, or those reported by Nicholas *et al.* (2007) who found significant differences in redness (a*) and yellowness (b*), but not lightness (L*), in 18-year-old blackwood from a single Tasmanian provenance planted across five sites in New Zealand.

In this study, broad differences in mean rainfall and rain-days did not to appear to contribute to heartwood colour variation in a consistent way. Virginstow 266/4/2 had poorer soils, lower mean rainfall, and fewer rain days (50) than Meunna 266/2/2 (75 days > 5 mm, Australian Bureau of Meteorology 2009), confirming that these variables, at

least within the ranges experienced in these trials, appear to have little effect on tree mean colour. In contrast the major difference in tree mean colour occurred between the

Table 6.1: Results of the mixed model analysis (F/Z values and levels of significance) for heartwood colour. Levels of significance for F/Z values are *** p<0.001, ** p<0.001, * p<0.05

	Lightness (L*)		Redness (a*)		Yellowness (b*)	
Fixed effects (F values)						
Trial	18.5	**	18.5	**	82.2	**
Family	4.2	**	5.2	**	3.8	**
Distance	59.7	**	224.7	**	187.5	**
Trial.Family	2.9	**	3.0	**	3.8	**
Distance.Trial	23.5	**	21.2	**	7.8	**
Distance.Family	2.1	*	2.9	**	2.6	*
Distance.Family.Trial	1.7	*	1.8	*	1.7	*
Random effects (Z values)						
Splinedist	0.0	ns	0.6	ns	0.4	ns
Splinedist.Trial	1.1	ns	0.9	ns	0.9	ns
Splinedist.Family	0.0	ns	1.1	ns	0.0	ns
Splinedist.Family.Trial	2.1	***	0.8	ns	1.2	ns
Tree	12.5	***	12.9	***	10.2	***
Distance.Tree	9.1	***	9.9	***	8.0	***
Splinedist.Tree	5.8	***	6.5	***	5.1	***

two Virginstow trials. Virginstow 266/4/1 had significantly lighter (L*), less red (a*) and less yellow (b*) mean heartwood colour than the other two trials (Figure 6.1). The two Virginstow trials are spatially intermixed and could be expected to differ little in climate or other abiotic environmental factors. The major differences were the *E. globulus* nurse crop and lower blackwood stocking in Virginstow 266/4/1. Such nurse crops are associated with increased competition for moisture and nutrients, and greater protection

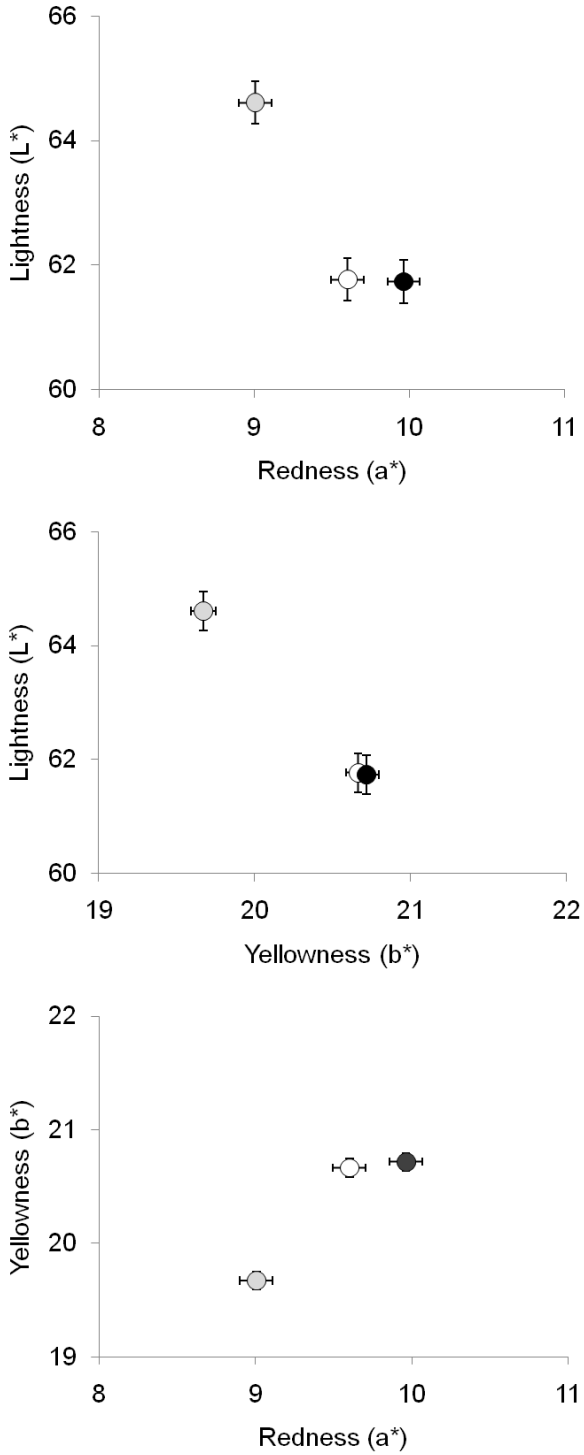


Figure 6.1: Predicted mean and standard errors for lightness (L*), redness (a*) and yellowness (b*) for the three trials Meunna 266/2/2 (○), Virginstow 266/4/1 (with nurse crop) (◍), and Virginstow 266/4/2 (●).

from frost for the blackwood (Neilsen and Brown 1996). Competition had a negative effect on blackwood growth in this trial, as it had the lowest mean diameter at breast height of the three trials (Chapter 4). The association of a lower growth rate and lighter mean colour in Virginstow 266/4/1 is not consistent with the common perception that faster-grown plantation timber is lighter coloured (Morrow 2007), or with the results of either Nicholas *et al.* (2007) or Bradbury (2005), who found no association between growth rate and heartwood colour. Other possible factors influencing wood colour in Virginstow 266/4/1 include competition and allelopathy from the nurse crop, which may be exacerbated by the relatively low rainfall and poor soils at Virginstow. Competition in mixed species plantations can have both positive and negative effects on growth (Forrester *et al.* 2004; da Silva *et al. In press*). *Eucalyptus globulus* is known to have allelopathic effects on soil nutrient availability, soil microbial flora, and the germination, growth and development of understorey species (Babu and Kandasamy 1997; Bagavathy *et al.* 2007). These results raise concerns about the use of nurse crops in blackwood plantations (Beadle *et al.* 2004), with further research needed to better understand the relationships between blackwood and potential nurse crop species.

In other species Rink (1987) found black walnut heartwood colour was more influenced by environment than genetics, with soil properties being implicated (Nelson *et al.* 1969; Maeglin and Nelson 1970), while Phelps and McGinnes (1983) suggested that increasing competitive or environmental stress resulted in increased production of polyphenols and hence darker coloured black walnut - a result opposite to that found at the Virginstow trials. Soil moisture and fertility were suggested as important

environmental factors influencing wood colour in *C. spruceanum* (Sotelo Montes *et al.* 2008), while intensive silvicultural treatment including soil cultivation, thinning and fertilising resulted in darker, redder wood in *Eucalyptus grandis* (Wilkins and Stamp 1990). All three trials in the current study received the same soil cultivation and fertiliser at planting (235 g per tree of 11:5:0 superphosphate/ammonium sulphate) (Neilsen and Brown 1996). The limited range of trials and treatments in this study provided interesting insights into the effect of environment on wood colour. However neither these results nor the available literature have yet provided a clear explanation of environmental factors controlling wood colour.

The significant genetic (family) effects on blackwood tree mean colour show that this trait is amenable to selection and breeding (Table 6.1), with generally lighter (e.g. 5F) and darker (e.g. 2A) coloured families apparent (Figure 6.2). However, while generally not as marked as the family effect, there were significant family by environment interaction effects on tree mean colour (Table 6.1). These appeared to be mainly driven by a change in the colour of particular families on specific sites (Figure 6.3). Therefore the optimization of colour expression through selective breeding may require the establishment of silviculture/environment specific breeding populations, unless families can be selected that have high colour-stability across a range of sites. Within the 16 families sampled, families 1L (light), 1N (dark) and 8B (medium) appeared the most colour-stable based on tree mean colour (Figure 6.3).

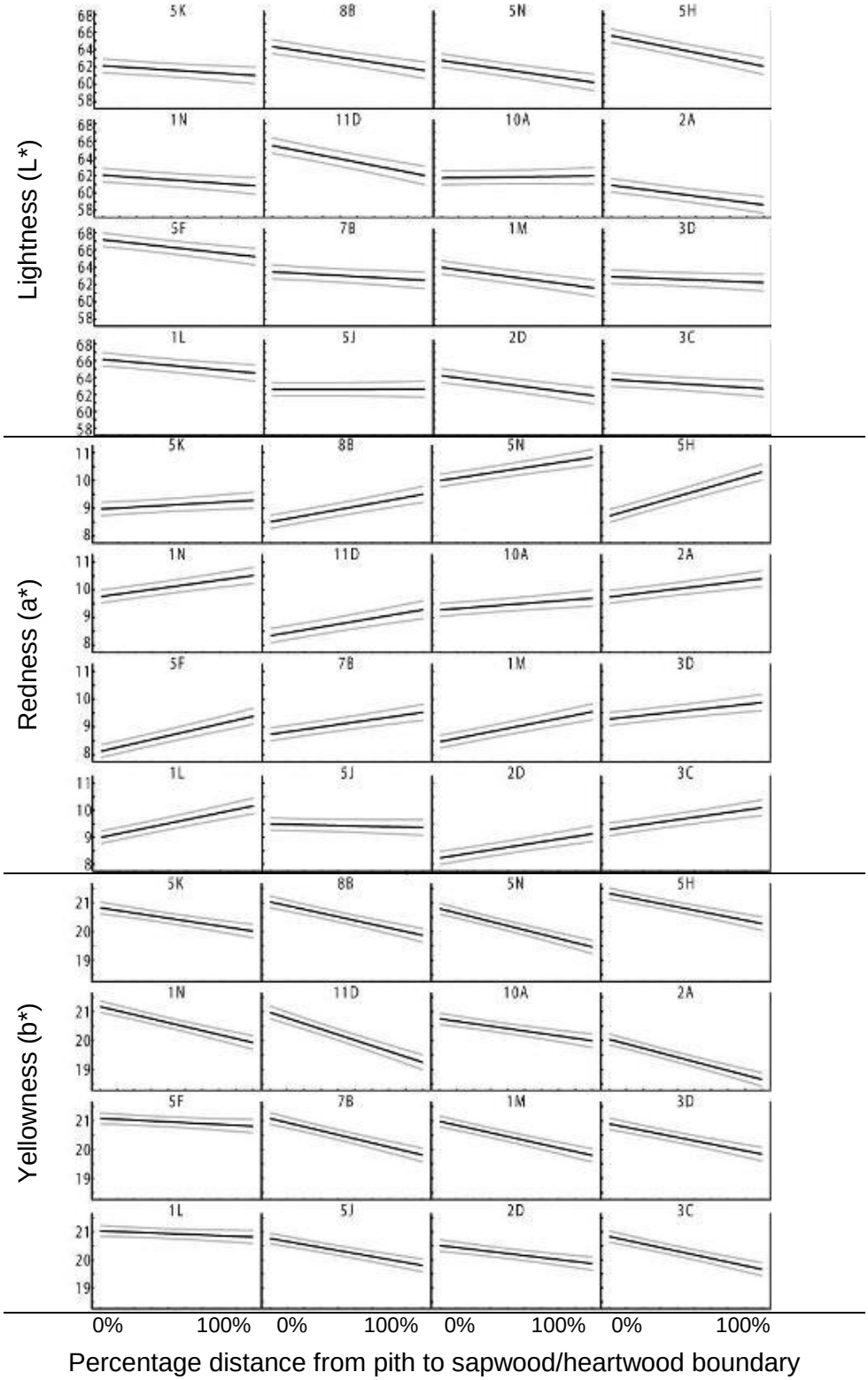


Figure 6.2: Radial colour trends from the pith to the sapwood/heartwood boundary, for the 16 families, showing the mean value and the standard error. Spline components were excluded from model

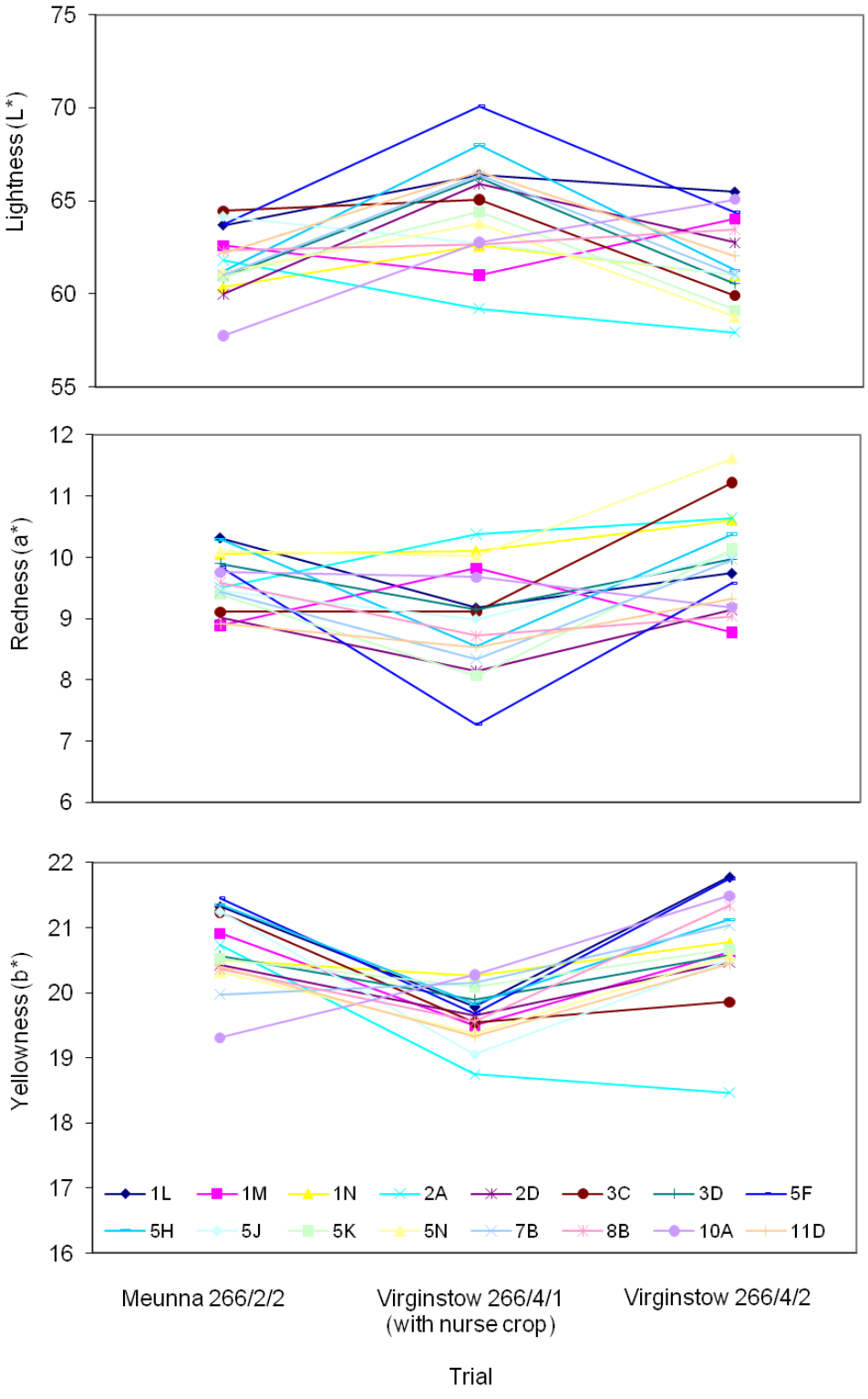


Figure 6.3: Significant family by environment interaction for tree mean colour across the 16 families

Within-tree wood colour variation

There were no significant non-linear patterns of radial heartwood colour variation, as indicated by the absence of significant spline or spline interaction effects, except for the three-way interaction for lightness, and the spline by tree effect which was significant for all traits. The spline was subsequently removed from the model for determining least squares means. Significant within-tree colour variation was observed for all traits but this was trial and family dependent (Table 6.1). There was also a small but significant three-way interaction indicating that the expression of family differences in within-tree radial colour variation was also dependent on the particular trial.

The significant effect of TRIAL on within-tree radial colour variation is shown in Figure 6.4. At Virginstow, both trials had similar radial colour patterns with decreasing lightness (L*) from the pith to the sapwood boundary, while at Meunna 266/2/2 there was a slight increase in lightness (L*) (Figure 6.4). Changes in redness (a*) at Virginstow mirrored the changes in lightness (L*) with increasing redness from the pith to the sapwood boundary, while at Meunna redness increased only slightly. Yellowness (b*) decreased from the pith to the sapwood boundary across all trials. Meunna 266/2/2 showed less within-tree radial colour variation compared with the two trials at Virginstow. Whether this was a response to better soils and/or higher rainfall is unknown, but does support observations by Harrison (1975a) that higher mean rainfall, more rain-days, and a cold-induced dormancy are necessary to produce more uniform coloured blackwood. Figure 6.4 also shows that while the two Virginstow trials had

similar within-tree radial colour patterns, they had significantly different tree mean colours. .

The significant DISTANCE by FAMILY interaction indicated a genetic effect on within-tree colour variation. The distinct patterns of within-tree colour variation between the 16 families are shown in Figure 6.2. Families showed differences in colour, as well as differences in the rate of change of colour, from the pith to the sapwood boundary. Of the 16 families sampled, none showed low within-tree colour variation and high colour stability across all sites, which may be desirable selection and breeding objectives necessary to achieve high between- and within-tree colour consistency. Using these objectives the best performing family was 3C, which showed uniform lightness (L*) and high colour stability across two sites (Figure 6.5a). The next best breeding objective for colour may be for the selection of families with a uniform pattern of within-tree colour variation across sites, even if mean tree colour values vary. This is best demonstrated by family 5N (Figure 6.5b), which shows uniform decreasing lightness (L*) from the pith to the sapwood boundary across the three trials. Family 10A is an example of a family that may be rejected in a breeding program due its inconsistent within-tree and across-site colour characteristics (Figure 6.5c). While heartwood colour is a key blackwood trait, other tree and wood properties will also be important in blackwood selection and breeding.

Conclusion

Significant genetic and environmental variation in between- and within-tree blackwood heartwood colour was detected across a small number of blackwood families

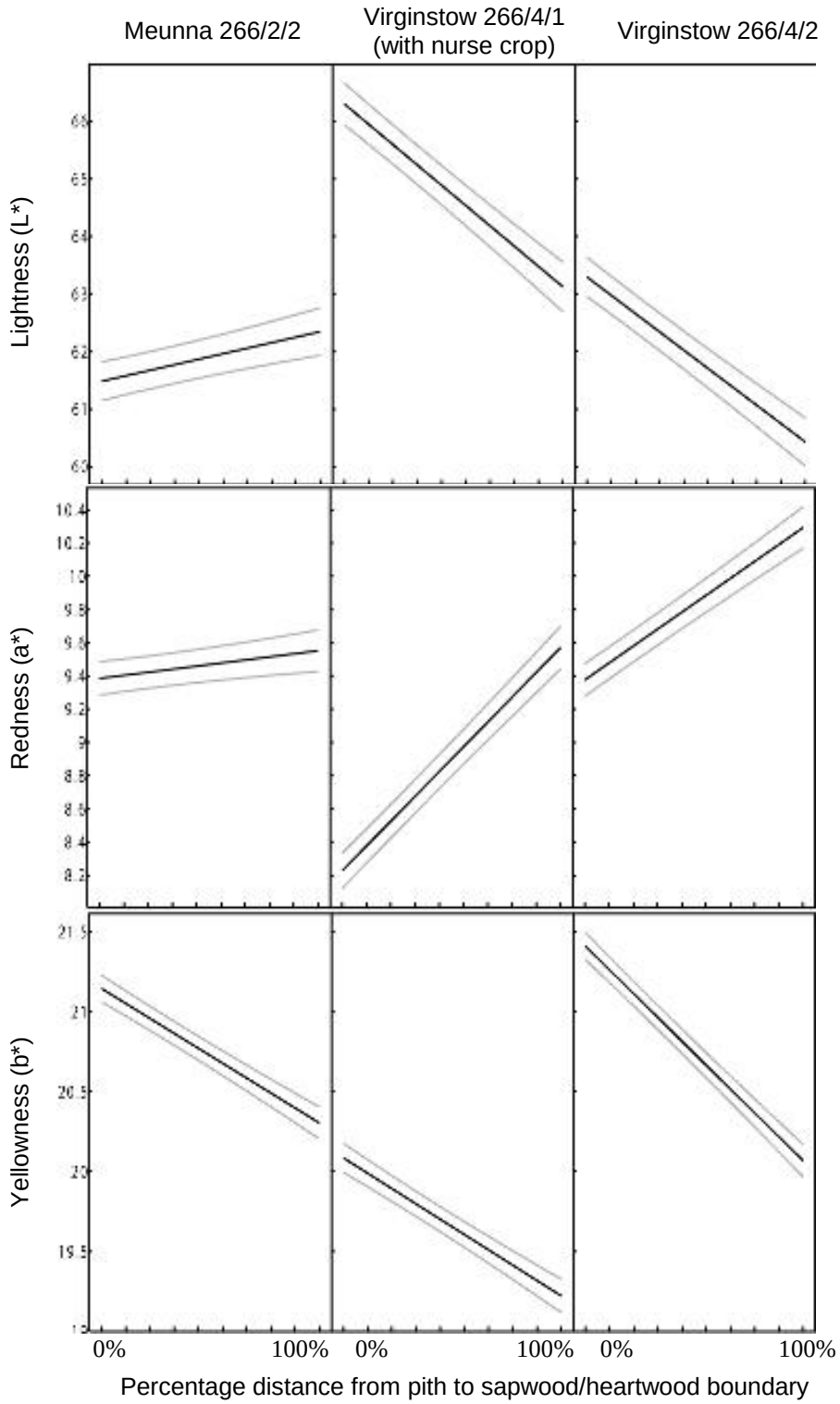


Figure 6.4: Radial colour trends from the pith to the sapwood/heartwood boundary, for the three trials, showing the predicted mean (-) and the standard error (-). Spline components were excluded from model

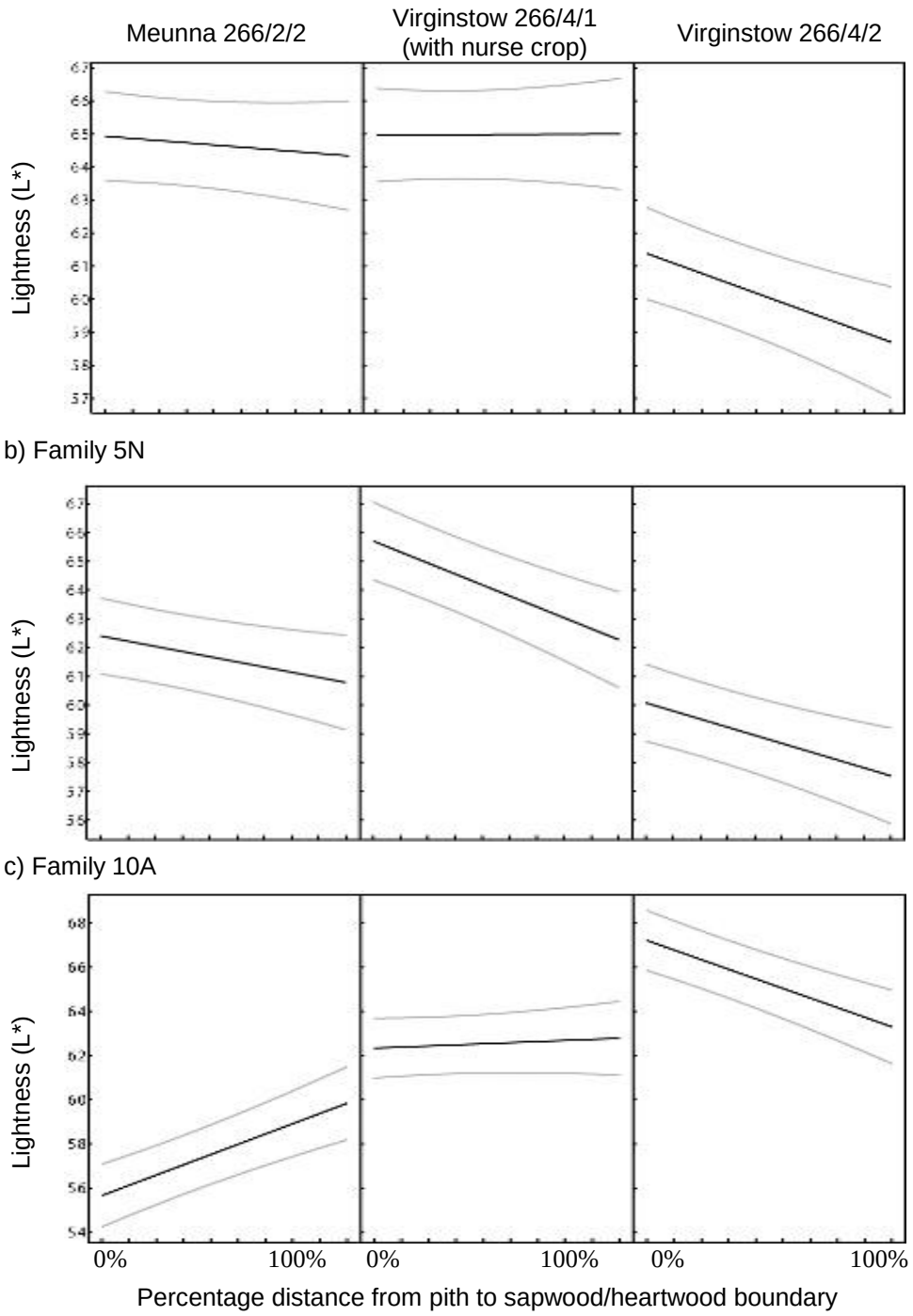


Figure 6.5: Within-tree changes in lightness (L*) from the pith to the sapwood/heartwood boundary for a) family 3C showing low within-tree colour variation and high colour stability across two sites; b) family 5N showing uniform within-tree colour variation but low colour stability across sites; and c) family 10A showing variable within-tree and across-site heartwood colour expression. Mean lightness (-) and standard error (-). Spline components were excluded from model

and sites. This indicates that selection and breeding for these important wood traits is possible. Selection and breeding for heartwood colour will present challenges, with many variables to manage such as tree mean colour, within- and between-tree variation, and colour stability across sites. The environmental factors that affect tree mean colour and between- and within-tree colour variation also appear to be complex and remain unknown. Based on the limited sites sampled in this study, factors such as mean annual rainfall, annual rain-days and soil properties by themselves appear to have little effect on tree mean colour, but may influence within-tree colour variation. There is also evidence to suggest that nurse crops may also affect tree mean colour.

Further work is required to quantify within-tree colour variation, particularly correlations between radial and tangential surface colour, and colour variation along the stem. The relationship between such variation and patterns observed in sawn boards, and veneers produced using various slicing methods, should also be examined (eg. Lu and Tan 2004; Marschner et al. 2005). Such research would help determine the best method of measurement and location in the stem to sample for heartwood colour and colour variation, and better correlate colour variation with industrial processing conditions. Changes in heartwood colour with different drying schedules should also be examined.

Chapter 7: Genetic and Environmental Variation in Wood Properties of *Acacia melanoxylon*

Introduction

Log diameter, percentage heartwood and heartwood colour are key factors determining the value of blackwood logs (de Zwaan 1982; Harington 2007), while traits such as wood density and stiffness impact on many timber uses, one of which is tonewood quality (Bucur 2006). Blackwood tonewood is predominantly used in acoustic guitars for the back, sides and neck (Evans 2007; Morrow 2007), and occasionally as soundboard material. Timber used for soundboards traditionally has low density and high stiffness, characteristics mostly associated with softwoods such as spruce (*Picea sp.*) and fir (*Abies sp.*), while back-and-side material generally has high visual appeal, higher density, good tonal acoustic properties, and good working and bending ability (Haines 2000; Bucur 2006; Wegst 2006). Density, strength and colour are also key requirements of timber used for flooring and furniture (Bootle 2005; Nolan *et al.* 2005).

The present chapter focuses on understanding the relative importance of the genetic and environmental effects on blackwood non-colour wood properties, and their correlations with heartwood colour. Non-colour wood properties of blackwood have been widely reported (Eckbo and Scott 1925; Greenhill and Dadswell 1940; Scott 1953; Kingston and Risdon 1961; Bolza and Kloot 1963; Sekhar and Kukreti 1979 ; Haslett 1986; Wilkins and Papassotiriou 1989; Caldersmith and Freeman 1990; Bucur and Chivers 1991; Harjono and Dunlop 1998; Bradbury 2005), based mostly on a limited

number of samples, often of unknown age and origin, and using various sampling and measuring methodologies. Despite apparent variation in many wood properties, little attention has been given to their potential genetic and environmental origin. What is apparent is that this variation has potential impacts on blackwood selection, breeding and utilisation. In this study, family-based progeny grown across three trials reported in Chapter 4 were used to assess the extent of genetic and environmental variation and their interactions on wood properties in blackwood.

Materials & Methods

Trials and genetic material

Three 18 year-old trials containing 16 open-pollinated single-tree Tasmanian blackwood families common to these trials were selected as discussed in Chapter 4. One trial was located at Meunna (Meunna 266/2/2) in north-west Tasmania, while two were located at Virginstow in northern Tasmania (Virginstow 266/4/1 and 266/4/2). The families in each trial were planted in a random complete replicate design. Two trials of pure blackwood (Meunna 266/2/2 and Virginstow 266/4/2) were planted with 5 replicates, each comprising single family line plots of 20 trees. The spacing was 3.0 m between rows and 4.2 m within rows. The other trial Virginstow (266/4/1), involved plantings of the same blackwood families in two replicates but with a nurse crop of one of the main plantation eucalypts grown in this area, *Eucalyptus globulus*. In this case, family plots were of approximately 0.2 ha in area (3.0 m spacing between and 4.2 m within rows for the blackwood and 2.1 m within rows for the eucalypt), comprising alternate rows of the single blackwood family and *E. globulus*, with a minimum of seven

rows of blackwood per family plot. The Virginstow trials were spatially intermixed with planting bays of the nurse crop trial alternated with planting bays of the pure blackwood trial, so that the primary difference between the trials was the presence of the nurse crop. None of the trials had received any thinning or pruning treatment. Meunna is a high rainfall site with deep fertile kraznozem soils, while Virginstow is a poor site for growing blackwood with relatively infertile soils and low rainfall (Allen 1992).

Sampling and measurement

Twelve trees from each of the 16 families were evenly distributed across 2-3 replicates in each trial for measurement and sampling. The replicates excluded from sampling were those where survival was low (Virginstow 266/4/2) or blackwood wildlings meant pedigrees could not be assured (Meunna 266/2/2). The 12-mm diameter stem cores were taken at breast height (1.3 m) in a north-south direction from each tree. . Trees were randomly selected from each family plot excluding trees with a diameter at breast height of <10cm. For each tree the following traits were measured: stem diameter at breast height (1.3 m), wood stiffness as estimated by standing tree time-of-flight (TOF) using a FAKOPP transit timer (www.fakopp.com) made on a one-metre length of the lower stem. Four TOF measurements were made of each tree, two each from both the north and south sides. Standing tree TOF has been successfully used as an indirect measure of wood stiffness in trees (Henson *et al.* 2004; Blackburn *et al. in press*). Stem core height was slightly adjusted where necessary to avoid including branch traces or other obvious defects in the cores. Cores were labelled and wrapped in plastic film before being refrigerated.

In the laboratory green cores were measured for weight, volume using the water displacement method (TAPPI 1989), total sapwood width as the sum of all sapwood from both sides of the core, heartwood width, percentage heartwood by area, and the count of visible annual growth rings within the sapwood. Cores were then oven-dried at 105 °C for two days. Oven-dried cores were then measured for weight and volume. The dried cores were then mounted into routed boards of *Pinus radiata* using polyvinyl acetate (PVA) glue, and put through a commercial sander to remove half of each core and expose a dressed radial surface suitable for colour measurement. Colour was measured using a Minolta CR400 Chroma Meter and the CIELAB colour space (Wyszecki and Stiles 1982) as detailed in Chapter 5. In brief, the CIELAB colour space is an international standard colour space which describes all the colours visible to the human eye using three coordinates representing the lightness of the colour (L *), its position between red and green (a * = redness) and its position between yellow and blue (b * = yellowness). Colour measurements of the heartwood were taken in 8-mm radial increments from the pith to the visible heartwood–sapwood boundary on either side of the pith, with care to avoid including sapwood in the heartwood colour data. Two single-sapwood colour measurements were taken from each core, one either side of the pith centred between the heartwood–sapwood boundary and the outer edge of the core under bark. Each sanded core was also assessed for the presence of any figured grain (e.g. fiddleback, birdseye, etc.).

Derived core traits were basic density (=oven-dry mass/green volume; kg m^{-3}), green density (= green mass/green volume kg m^{-3}), green moisture content (GMC = 100*(green mass – oven-dry mass)/oven-dry mass; %). The Fakopp (FK; μs) values were

converted to time-of-flight ($m.s^{-1}$) using the mean of the four Fakopp measurements using the formula TOF = 1,000,000/(FK-9.4) where 9.4 is the time correction factor (Fakopp *online*). For each core, the mean heartwood and sapwood lightness (L*), redness (a*) and yellowness (b*) were calculated. Within-core heartwood colour variation was determined by calculating the distance (ΔE76) between all heartwood colour measurements using the formula $\Delta E76 = \sqrt{\Delta L^2 + \Delta a^2 + \Delta b^2}$ (Wyszecki and Stiles 1982). For each core both the mean and maximum ΔE76 were calculated as measures of colour variation. For each core the difference between the mean heartwood and mean sapwood colours was also calculated.

Data analysis

The significance of trial, family and their interaction on wood properties was tested by fitting a mixed linear model to stem core data using Proc MIXED of SAS (version 9.1, SAS Institute Inc. 2004). The model fitted was:

Equation 7.1: Y = TRIAL + FAMILY +TRIAL.FAMILY + *REP(TRIAL)* + *PLOT* + *RESIDUAL*

where TRIAL is the fixed trial effect, FAMILY is the fixed family effect and TRIAL.FAMILY is the fixed trial by family interaction effect. *REP(TRIAL)* is the random replicate-within-trial effect and *PLOT* is the random plot-within family within trial effect. In a separate analysis stem diameter was included as a covariate in the model to test what effect if any there was of growth rate. The random *REP(TRIAL)* effect was used as the error to provide an approximate test of the fixed TRIAL effect, and when significant the Tukey-Kramer test for multiple comparisons was used to determine which

trials were significantly different ($p < 0.05$). The FAMILY and TRIAL.FAMILY effects were tested using the random *PLOT* term as the error.

To calculate Pearsons correlations between traits at a family (i.e. genetic) and phenotypic level, the tree level data was firstly standardised using PROC STANDARD of SAS such that each site had a mean of zero and a standard deviation of one. Overall family arithmetic means for each trait were then calculated and the Pearsons correlations amongst traits calculated using these means with PROC CORR of SAS. The phenotypic correlations were calculated based on the standardised tree-level data and represent the pooled, within-trial phenotypic correlations amongst traits. In addition to pair-wise significance levels, a Bonferroni adjustment for a $p = 0.05$ level of significance across all comparisons within a correlation type was also used ($p < 0.00064$).

Results

Genetic and environmental variation

Stem diameter and figured grain

The mean diameter of the sampled trees was 15.3±4.2 cm (Table 7.1). The nurse crop trial, Virginstow 266/4/1, had the lowest mean diameter of 13.8 cm while Meunna 266/2/2 had the highest at 16.0 cm. However the difference between trials was not statistically significant (Table 7.1). This was also the case when all trees from the 16 families were measured, rather than the smaller sample of larger (≥ 10 cm diameter) trees used in this study (Chapter 4). The differences in stem diameter between families based on the ≥ 10 cm subsample were significant, but there was no significant trial by

family interaction (Table 7.1). Only one stem core displayed traces of figured (fiddleback) grain character on the radial surface.

Heartwood and sapwood

Mean (±s.d.) heartwood width was 86.7±33.2 mm (range 0 to 206 mm), mean total sapwood width was 53.1±17.5 mm (range 17 to 168 mm) and the mean percentage heartwood was 38.6±13.4 % (range 0 to 77%). Sapwood annual ring count ranged from three to 12 years with a mean of 6.5, but could only be assessed on 39% of the cores due to indistinct annual rings. Trial had no significant effect on any of these three traits. Family had a significant effect on percentage heartwood and sapwood width (Table 7.1). However, despite a significant family effect on stem diameter there was no significant family effect on the absolute amount of heartwood. Therefore the significant difference in stem diameter was due to differences between the families in the sapwood width. This trend was consistent with the percentage heartwood being significantly negatively correlated with sapwood width at the family level, but not with heartwood width (Table 7.2). When diameter was fitted as a covariate, there was a significant difference between families in the percentage heartwood ($F_{15, 71} = 3.6$, $p < 0.001$), indicating that, at least in a linear sense, growth rate alone did not explain the difference in percentage heartwood between families. There were no significant trial by family interaction effects on any of these three traits.

Table 7.1: Stem core properties together with F values and significances of the fixed terms from the mixed model analysis

	Mean	Std Dev	Trial $F_{2,6}$		Seedlot $F_{15,71}$		Trial*Seedlot $F_{30,71}$	
Stem diameter (cm)	15.3	4.2	3.6		1.9	*	0.4	
Sapwood width (mm)	53.1	17.5	2.9		4.1	***	0.9	
Heartwood width (mm)	86.7	33.2	1.7		1.1		0.7	
Heartwood (%)	38.6	13.4	1.7		2.1	*	1.0	
Green density (kg m^{-3})	1000.8	104.7	22.6	**	2.4	**	2.0	**
Basic density (kg m^{-3})	488	51	9.7	*	4.5	***	1.8	*
Green Moisture Content (%)	106.3	22.5	83.4	***	2.6	**	1.6	
Time of Flight (m s^{-1})	3383	252	3.0		4.2	***	2.5	**
Heartwood lightness (L*)	62.7	4.8	14.4	**	4.0	***	2.6	**
Heartwood redness (a*)	9.5	1.4	11.6	**	4.0	***	2.0	**
Heartwood yellowness (b*)	20.3	1.2	18.2	**	4.2	***	3.6	***
Sapwood lightness (L*)	82.2	3.5	4.4		1.4		0.9	
Sapwood redness (a*)	3.0	1.1	6.3	*	1.1		1.2	
Sapwood yellowness (b*)	15.2	1.4	0.2		0.9		0.9	
Mean within-core heartwood colour variation (ΔE)	4.5	1.6	3.0		1.6		1.1	
Maximum within-core heartwood colour variation (ΔE)	10.9	4.7	0.5		1.2		1.0	
Sapwood to heartwood mean colour difference (ΔE)	21.4	4.4	0.3		2.9	**	2.0	**

Levels of significance: *** p <.001, ** p <.01, * p <0.05.

Green/basic density and green moisture content

Green density had a mean of 1001±105 kg m^{-3} (range 584 to 1160 kg m^{-3}), while basic density had a mean of 488±51 kg m^{-3} (range 332 to 635 kg m^{-3}). Both traits showed significant trial and family effects, as well as significant trial by family interactions (Table 7.1). The significant trial effects were due to the nurse crop trial Virginstow 266/4/1 having significantly lower green density than the other two trials, and Meunna 266/2/2 having significantly lower basic density than either of the Virginstow trials (Table 7.3). The significant interaction effects on basic density were due to changes in

Table 7.2: Pearsons phenotypic (above diagonal) and genetic (below diagonal) correlations (*r*). Phenotypic correlations were standardised by trial and pooled across trials (n = 561-566), and family (i.e. genetic) correlations were pooled across trial family means (n = 16). Significance levels are * *p* <0.05, ** *p* <0.01, * *p* <0.001, and the Bonferroni adjustment for 0.05 level of significance for multiple comparisons (*p* <.0006) is shown in bold**

	Stem diameter	Sapwood width	Heartwood width	Heartwood (%)	Basic density	Green density	Green Moisture Content	Time of flight	Heartwood lightness (L*)	Heartwood redness (a*)	Heartwood yellowness (b*)	Maximum colour variation (ΔE)	ΔE sapwood to heartwood
Stem diameter		**0.38** ***	**0.83** ***	**0.34** ***	-0.01	0.10 *	**0.14** ***	0.01	-0.12 **	0.06	**0.22** ***	**0.29** ***	0.10 *
Sapwood width	0.70 **		-0.01	**-0.66** ***	**-0.17** ***	**-0.31** ***	-0.13 **	0.13 *	**0.24** ***	**-0.26** ***	**0.18** ***	-0.06	**-0.22** ***
Heartwood width	0.77 ***	0.13		**0.71** ***	0.07	**0.25** ***	**0.20** ***	-0.02	**-0.20** ***	0.14 ***	**0.19** ***	**0.38** ***	**0.15** ***
Heartwood (%)	-0.19	**-0.81** ***	0.44		**0.18** ***	**0.41** ***	**0.24** ***	-0.12 **	**-0.33** ***	**0.28** ***	-0.01	**0.35** ***	**0.27** ***
Basic density	-0.05	-0.35	0.17	0.46		**0.70** ***	**-0.44** ***	-0.02	**-0.39** ***	**0.27** ***	**-0.27** ***	0.13 ***	**0.29** ***
Green density	-0.25	-0.43	0.01	0.46	**0.80** ***		**0.29** ***	**-0.21** ***	**-0.50** ***	**0.41** ***	**-0.19** ***	0.15 ***	**0.30** ***
Green Moisture Content	-0.23	0.02	-0.24	-0.15	-0.65 **	-0.07		-0.27 ***	-0.13 **	**0.15** ***	0.11 *	0.01	0.10 *
Time of flight	0.07	0.27	-0.10	-0.27	-0.12	-0.35	-0.26		0.24 ***	-0.23 ***	0.08	-0.02	-0.22 ***
Heartwood lightness (L*)	0.11	0.20	0.09	-0.18	-0.44	-0.66 **	-0.11	0.44		**-0.48** ***	**0.48** ***	**-0.27** ***	**-0.75** ***
Heartwood redness (a*)	-0.03	-0.20	0.15	0.34	0.22	0.52	0.32	-0.15	-0.48		-0.02	0.05	**0.45** ***
Heartwood yellowness (b*)	0.10	0.28	0.00	-0.27	-0.47	-0.41	0.24	0.49	**0.79** ***	-0.26		**-0.18** ***	**-0.30** ***
Maximum colour variation (ΔE)	-0.06	-0.31	0.25	0.44	0.01	0.04	0.11	0.02	-0.37	0.36	-0.48		**0.19** ***
ΔE sapwood to heartwood	-0.14	-0.26	-0.03	0.28	0.53 *	0.68 **	-0.03	-0.33	**-0.90** ***	0.42	-0.72 **	0.43	

Table 7.3: Mean stem core values for the three trials for traits where significant trial effects were observed. Values in the same row having the same letter do not differ significantly ($p < 0.05$) following the Tukey-Kramer adjustment

	Trial		
	Meunna 266/2/2	Virginstow 266/4/1 (nurse crop)	Virginstow 266/4/2
Green density (kg m^{-3})	1044a	924b	1020a
Basic density (kg m^{-3})	465b	497a	502a
Green moisture content (%)	126a	86c	104b
Heartwood lightness (L*)	61.7b	64.3a	61.8ab
Heartwood redness (a*)	9.6ab	9.1b	9.8a
Heartwood yellowness (b*)	20.8a	19.7b	20.8a
Sapwood redness (a*)	3.3a	2.5b	3.0ab

rank between families across trials, with two families (1M and 7B) showing particularly marked changes in rank in the nurse crop trial Virginstow 266/4/1 (Figure 7.1a). However many families retained their basic density ranking across the trials; especially between the pure blackwood trails at Meunna 266/2/2 and Virginstow 266/4/2, demonstrating the significant overall family effect on this trait. Green moisture content (GMC) had a mean of 106±22 % (range 51 to 176 %).

There were significant trial and family effects on GMC, and no significant interaction effects (Table 7.1). The trial effect was very strong with significant differences between all three trials (Table 7.3). Mean GMC was greatest at Meunna 266/2/2, the highest rainfall trial, and lowest in the nurse crop trial Virginstow 266/4/1 (Table 7.3). When fitted as a covariate in the mixed model, stem diameter had a significant positive effect on both green density ($F_{1,438} = 7.6$, $p = 0.006$) and GMC ($F_{1,438} = 12.2$, $p = 0.0005$), but not on basic density ($F_{1,438} = 0.0$, $p = 0.948$).

Time of flight

The mean standing tree time–of-flight (TOF) was 3383±252 m s^{-1} (range 2664 to 4513 m s^{-1}). There was a significant family effect and a significant interaction effect on TOF (Table 7.1). The significant interaction effect was due to both changes in

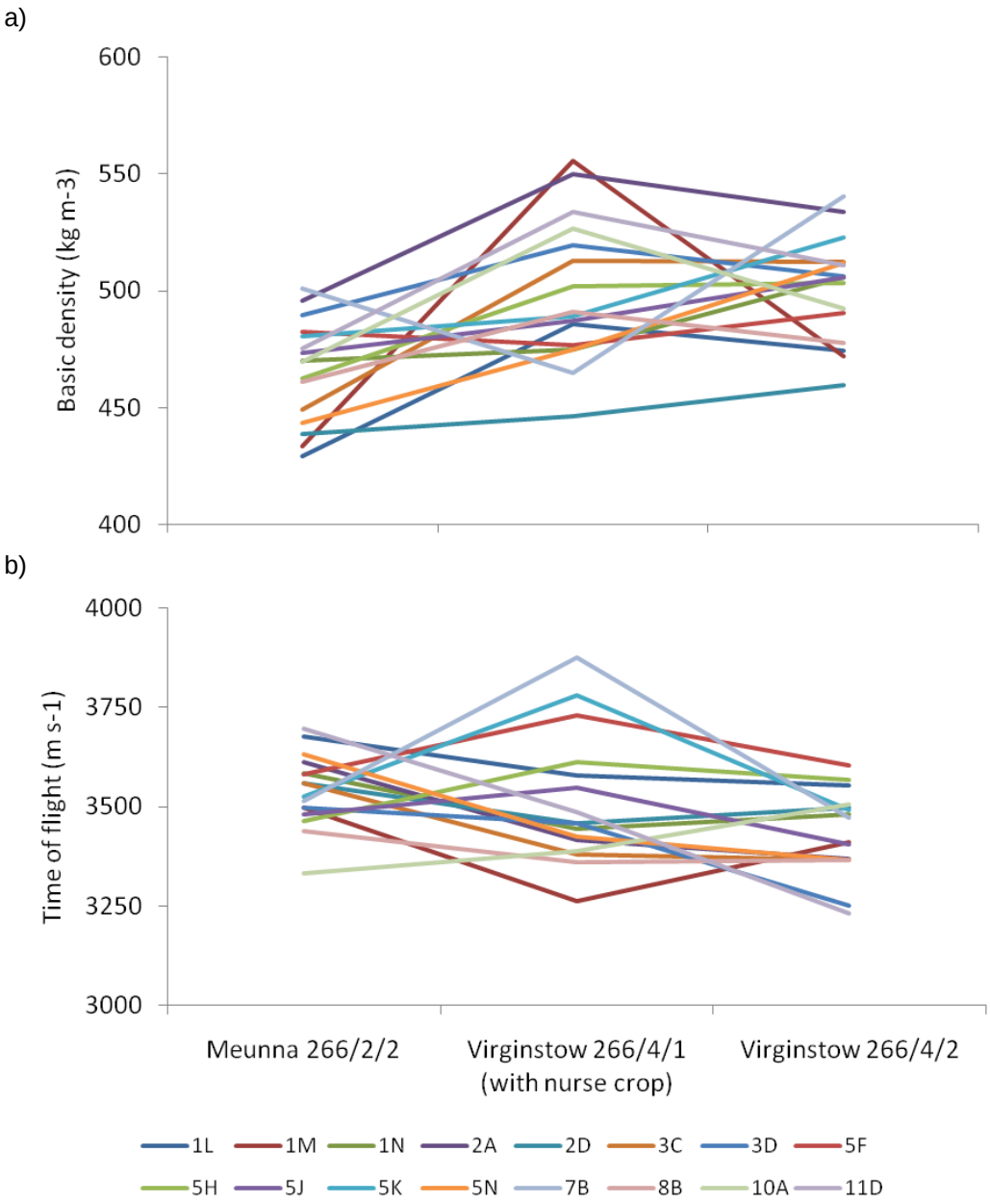


Figure 7.1: Significant trial by family interaction effects for a) basic density and b) standing tree time of flight. Changes in family least squares means across trials are shown

family ranking between trials as well as changes in variation in TOF, particularly in the nurse crop trial Virginstow 266/4/1 (Figure 7.1b).

Heartwood colour

Significant trial, family and interaction effects on all mean heartwood colour traits were found (Table 7.1), consistent with the results of Chapter 6 where individual colour measures were analysed using a mixed model which fitted a cubic spline to model within-core variation. The significant trial effect was due to the heartwood from the nurse crop trial Virginstow 266/4/1 being lighter, less red and less yellow than the heartwood from the other trials (Table 7.3). Sapwood colour showed little trial or family variation (Table 7.1). The only significant effect detected was a trial effect on sapwood redness, which was due to the nurse crop trial Virginstow 266/4/1 having less red sapwood, consistent with the trend in heartwood (Table 7.3). There were no significant trial, family or interaction effects on either within core mean or maximum ΔE76 values (Table 7.1).

Correlations

At the phenotypic level within trials, correlations indicated that faster growing trees (i.e. stem diameter) had more sapwood and heartwood, greater percentage heartwood, and greater green moisture content (Table 7.2). However at the family level (i.e. genetic level) these correlations were only significant for sapwood and heartwood width, with faster growing families having more heartwood and sapwood (Table 7.2). There was no significant correlation between growth rate and basic density or time of flight at either the phenotypic or family level (Table 7.2). There were many significant correlations amongst the wood property traits at the

phenotypic level but few at the family level (Table 7.2). At the phenotypic level, time of flight was weakly negatively correlated with green moisture content (r = -0.27) and green density (r = -0.21), but not basic density (r = -0.02), despite basic and green density being positively correlated (r = 0.70). At the phenotypic level, heartwood colour was weakly correlated with diameter growth but was correlated with percentage heartwood, as well as basic and green densities. Faster growing trees tended to have darker (L*) and more yellow (b*) heartwood. However when the joint correlation with percentage heartwood is accounted for by a partial correlation analysis, only the phenotypic correlation between diameter and heartwood yellowness was significant ($r_{partial}$ = 0.24, $p < 0.001$). Trees with higher basic and green density tended to have darker (L*), more red (a*) and less yellow (b*) heartwood, however at the family level these correlations were only significant between green density and heartwood lightness (L*).

Discussion

Genetic and environmental variation in wood properties

Despite the limited genetic and environmental sampling, the present study has shown that both genetics (seedlot) and environment (trial) can significantly affect most wood properties in blackwood. In many cases there were significant interaction effects. These interaction effects usually involved changes in the ranking of families, with most changes associated with differences in family performance in the nurse crop trial Virginstow 266/4/1.

The present study suggests that the absolute amount of heartwood in blackwood is driven simply by growth rate. However the relative amount of heartwood is related

more to variation in sapwood width, which has a genetic basis and appears to drive the differences between families in percentage heartwood. These results suggest that improvements in both growth rate and percentage heartwood can be independently made through genetic selection. Percentage heartwood has also been shown to be under genetic control in other hardwood species including other *Acacia* species (Woeste 2002; Searle and Owen 2005; Bhat *et al.* 2007), but not previously in blackwood. If percentage heartwood and heartwood colour is to be assessed by breeders, then it is important to understand at what tree size and age heartwood formation in blackwood commences and these traits can be first assessed. This also requires early age assessments being associated with harvest-age measures i.e. strong age-to-age correlations. For breeders these considerations affect the assessment and breeding cycle times (White *et al.* 2007).

It is possible that tree size rather than age is more significant in the commencement of heartwood production in blackwood. This is evidenced by comparing the results from the current study with previous studies. Two previous studies of blackwoods of similar or younger ages have shown trees of larger stem diameter with greater percentage heartwood than the current study. A 10 year-old progeny trial had mean diameters of 16.6 to 20.5 cm with mean percentage heartwood of 42 to 52% (Nicholas *et al.* 1994b); while thinnings from a 17 year-old silvicultural trial had a mean diameter of 24.1 cm and mean percentage heartwood of 54% (Nicholas *et al.* 2007). This compares with the current study of 17 year-old blackwood with a mean diameter of 15.3 cm and mean percentage heartwood of 38.6%. The best performing provenance in the Nicholas *et al.* (1994b) study was the same as that used in the silvicultural trial (Nicholas *et al.* 2007), where the smaller,

thinning material was sampled. While this comparison is confounded by genetic and sampling effects, it does indicate that stem diameter is the dominant factor controlling the initiation of heartwood production. This hypothesis needs to be tested with age-age correlations in percentage heartwood across a range of genetic material. No age-age correlations in percentage heartwood in blackwood or any other species are known.

Green and basic densities, green moisture content, and time of flight values in this study were within the ranges previously reported, with the basic density range being similar to a 17 year-old silvicultural trial involving a single Tasmanian blackwood provenance (291 – 633 kg m^{-3}) (Nicholas *et al.* 2007). The variation in these wood traits, even within the limited range of material sampled in this study, highlights the issue of product consistency in blackwood, particularly the very low basic densities (<400 kg m^{-3}) that may be associated with low strength and low hardness. The significant differences between families for these traits indicates that genetic gains are possible, although the significant trial (excluding TOF) and GxE interaction (excluding GMC) effects show that greater understanding of the environmental factors affecting these traits is needed. Significant genetic variation in basic density has previously been found in blackwood (Nicholas *et al.* 1994b) and other acacias (Searle and Owen 2005; Hai *et al.* 2007), with significant differences found between provenances (Hai *et al.* 2007). Much of the significant interaction effect on basic density in the current study was due to major reaction by a few families (eg. 1M and 7B) to conditions in nurse crop trial Virginstow 266/4/1.Most families however, showed reasonable stability in ranking across the three trials (Figure 7.1a), demonstrating the significant genetic effect on basic density. This was

not the case with TOF where the significant interaction effects were the result of changes in order of rank across the trials for many families, as well as increased variation in TOF between the families in the nurse crop trial Virginstow 266/4/1 compared with the two pure blackwood trials. Identifying genetic material that demonstrates stable wood property rankings across a range of sites will be important if gains in selection and breeding programs are to be fully realised.

The significant differences between the pure blackwood trials (Meunna 266/2/2 and Virginstow 266/4/2) clearly show that broad-scale environmental factors can affect blackwood basic density and green moisture content but potentially less so heartwood colour or time-of-flight. Significant environmental effects on basic density as well as heartwood colour in blackwood have been previously reported (Harrison 1975b; Harrison 1975a; Nicholas *et al.* 2007). Harrison (1975a) found no significant variation within but significant variation between regions in heartwood colour in blackwood plantations across South Africa. The environment that produced the best (dark and uniform) colour was a site well watered during the growing season, but which had a definite dormant period created by low rainfall and low temperatures, as well as a frost period. The total amount of rainfall during the growing season was less important than the number of rain days. The results of Harrison (1975a) were only partially supported by New Zealand studies where Nicholas *et al.* (2007) found significant differences in heartwood colour between two sites close together, assumed to have similar climates; three more distant sites, presumed to have greater differences in climate, were not significantly different in heartwood colour.

Nicholas *et al.* (2007) reported similar site differences for basic density to that for heartwood colour. Higher basic density on drier sites has been observed in *Acacia mangium* (Awang and Taylor 1993) and *Eucalyptus globulus* (Raymond and Muneri 2000), which is consistent with the present results as Virginstow is drier than Meunna. However, rainfall differences were not identified as the possible cause of site differences in basic density observed by Nicholas *et al.* (2007). Downes *et al.* (2006) found a significant reduction in wood basic density in *Eucalyptus globulus* and *E. nitens* under irrigation that was not related to diameter growth. This is consistent with the current study where significant differences in basic density between trials were not associated with significant differences in diameter growth. However, the lack of significant difference in basic density between the two Virginstow trials, despite a significant difference in wood green moisture content, suggests that factors other than moisture availability are also influencing blackwood basic density.

Mean heartwood colour values were within the range previously recorded (Nicholas *et al.* 1994b; Bradbury 2005; Nicholas *et al.* 2007). The significant trial, family and interaction effects for all heartwood colour traits are consistent with that reported in Chapter 6, and demonstrates the complex nature of heartwood colour expression in blackwood. Despite the significant effect of site and family on the linear change in heartwood colour from the pith to sapwood reported in Chapter 6, the holistic measures of within-tree colour variation used in the current study (mean and max ΔE), showed no significant family or trial effects, suggesting they have little power to detect biologically significant differences in within tree colour variation. Indeed, this lack of power could explain the failure of Sotelo Montes *et al.* (2008) to

detect significant site and seedlot effects on within-tree colour variation in *Calycophyllum spruceanum* using similar methods.

The significant difference in heartwood colour between the two Virginstow trials was due to the presence or absence of the nurse crop. The only other differences detected between these trials were for green density and green moisture content. The presence of the nurse crop resulted in lighter, less yellow and less red wood as well as wood with lower green moisture content also reflected in lower green density. This relationship between colour change and moisture content associated with the presence of a nurse crop is unlikely to be causal and probably represents independent responses of the colour traits and green moisture content. This hypothesis is based on: i) there was no difference in heartwood colour between the two pure blackwood trials despite a significant difference in green moisture content of the wood (Table 7.3); ii) despite significant differences between families in both heartwood colour and green moisture content there were no significant correlations between these traits at the family level (Table 7.2); and iii) despite significant phenotypic correlations between green moisture content and the colour traits between trees within sites which were consistent with the nurse crop trend, the magnitude of the correlations was low ($r < 0.16$; Table 7.2). So, while Harrison (1975a) reported that blackwood grown in South Africa on wetter sites produced darker wood, the present study suggests this is unlikely to be due to wood moisture content *per se*. It is possible that the increased competition from the *E. globulus* nurse crop decreased the water available to the blackwoods which affected the green moisture content of the wood, but these results suggest that other effects of competition or even allelopathy are responsible for the adverse effects on heartwood colour (see Chapter 6 for further discussion).

Correlations

Significant positive phenotypic correlations between diameter growth and percentage heartwood in this study supports previous studies in blackwood (Nicholas *et al.* 1994b; Nicholas *et al.* 2007), and demonstrates that at the phenotypic level faster growing trees will produce more heartwood compared to sapwood. However, in the present study the genetic-based differences between families in this proportion was due to differences in the absolute amount of sapwood rather than heartwood. In the present study larger trees had slightly higher green moisture content, but this trend was not statistically significant in the study by Nicholas *et al.* (1994b). The lack of significant genetic and phenotypic correlations between diameter growth and other important wood properties such as basic density and time-of-flight (Table 7.2), suggests that increasing growth rates through either selection and breeding, or intensive management, should have little impact on these traits. This supports previous studies that have found no significant negative phenotypic correlations between diameter growth and basic density in blackwood (Nicholas *et al.* 1994b; Bradbury 2005; Nicholas *et al.* 2007) and other Acacias (Kim *et al.* 2008; Hai 2009). However Hai (2009) found a significant negative genetic correlation between growth rate and wood stiffness measured on dried boards sawn from *Acacia auriculiformis*.

The green and basic densities were significantly positively correlated at the phenotypic and family levels. There was a clear trend at both levels for wood with high basic density to have lower green moisture content, a trend also reported by Nicholas *et al.* (1994b). Time of flight measurements on the standing trees were weakly negatively correlated with moisture content and green density but not basic density. There are no known comparable studies of time-of-flight in blackwood with

which to compare the present data. However standing tree radial (rather than longitudinal) TOF values for *Acacia mangiu*m were lower than values in the current study (Yamamoto *et al.* 1998). Significant positive correlations between standing tree time-of-flight and wood density have been reported in *Acacia mangium* and other hardwood species (Yamamoto *et al.* 1998; Henson *et al.* 2004; Blackburn *et al. in press*). As time-of-flight is an indirect measure of board stiffness, the significant family variation in this trait and its independence from basic density is of potential interest in tonewood markets. The variation in blackwood basic density found in this and other studies together with the apparent variation in wood stiffness found in this study, indicates the potential of blackwood to be used in a range of tonewood applications such as soundboards as well as back-and-side sets in acoustic guitars where different wood properties are required (Haines 2000; Wegst 2006; Morrow 2007).

The present study revealed a weak phenotypic association between growth rate and several aspects of heartwood colour. There was also a relationship between the percentage heartwood and several of the heartwood colour traits. Once this was accounted for there was only the tendency for larger trees to have more yellow heartwood that remained significant. Nicholas *et al.* (1994b; 2007) found no significant phenotypic correlations between diameter growth and heartwood colour. However, in an independent study of native blackwood regrowth of variable age, Bradbury (2005) also reported a significant positive correlation of tree diameter and with heartwood yellowness (b*). A similar correlation has also been found in the Amazonian hardwood *Calycophyllum spruceanum* (Sotelo Montes *et al.* 2008), but not in *Eucalyptus dunnii* (Vanclay *et al.* 2008) or teak (*Tectona grandis*) (Moya and

Berrocal 2010). In all cases correlations between diameter growth and heartwood colour were weak ($r < 0.23$), so that contrary to popular belief (p. 19, Morrow 2007), increased growth rate in blackwood does not appear to lead to major changes in heartwood colour. However, there is a clear trend at the phenotypic (most significant) and family (only one significant) level for trees with greater percentage heartwood, greater basic and green density to have darker, redder and less yellow heartwood colour, all of which are favourable trends to meet general market requirements. These trends are consistent with those previously reported for basic density in blackwood (Nicholas *et al.* 1994b) and *Calycophyllum spruceanum* (Sotelo Montes *et al.* 2008).

Conclusions

Significant genetic and environmental variation, together with genetic by environmental interaction was found in many blackwood wood properties, even within the small genetic and environmental sample used in this study. Genetic gains in traits such as percentage heartwood, basic density, standing tree time-of-flight and heartwood colour should be possible, although significant GxE interactions for some traits will complicate capturing these gains. Families showed varying levels of stability in ranking across trials for individual wood traits, so that identifying and selecting genetic material of high and stable rank across sites would be advantageous for deployment. Both broad-scale or local environmental effects on wood properties were apparent across the three trials in this study. The local effect was due to the presence of a *Eucalyptus globulus* nurse crop which appeared to have a significant effect on a number of wood properties, including heartwood colour. Whether this

effect is nurse-crop species dependant, and occurred through competitive and/or allelopathic effects remains unknown.

The present study suggests that increasing blackwood growth rate under intensive plantation management or through family selection should result in increased heartwood production but have little effect on other important wood properties. While significant site and family effects were demonstrated for many important wood properties in this study, further advances will depend upon large scale sampling to better understand environmental and genetic effects on wood properties. At the environmental level, more sites need to be assessed as well as the impact of co-occurring species. Indeed, the finding that the nurse crop had an adverse effect on some wood properties needs further investigation so as to understanding the mechanisms involved. It also means that the already complicated silviculture required in plantations with nurse crops is now confounded with potential adverse effects of the nurse crop on wood properties. At the genetic level, it is clear that greater sampling of the native range of blackwood is required to better understand the geographic trends in genetic variation plus estimate the genetic parameters such as heritabilities and genetic correlations required to predict the genetic gains achievable.

Considering the variation in key wood properties such as heartwood colour, basic density and potentially wood stiffness found in blackwood in this and other studies, a major issue for blackwood breeders and growers is the lack information on market requirements for blackwood timber at the level of individual wood properties. These requirements are likely to vary between market sectors, and change with consumer preferences. Generally darker heartwood colours and higher basic density are

preferred; however more market research is needed to allow breeders and growers to produce blackwood with more consistent wood properties better matched to market requirements.

Chapter 8: General Discussion

For a commercial species with prospects for further domestication and use in plantations, considerable genetic and phenotypic variation in growth, form and wood properties was found to exist within the Tasmanian blackwood population. This genetic variation presents opportunities in selection and breeding to achieve improved growth rates, stem form and deliver improved, more consistent wood quality. Reasonable levels (moderate to low) of narrow-sense heritabilities for growth and form respectively also support these opportunities for genetic gain. However the current study has only shown this potential based on a limited selection of samples within the cool temperate Tasmanian population of blackwood.

The current study confirms the naturally poor form of open-grown, unmanaged plantation blackwood. In order to grow clear, straight-grain, knot-free timber in plantations, blackwood must be pruned during the early years of the rotation. However, this study has also shown that even in open-grown, unmanaged plantations, a small percentage of trees (~2%) displayed strong apical dominance resulting in excellent stem form. Unfortunately the incidence of this trait was too low to allow the extent of its genetic and environmental variation to be determined. Further research in this area is warranted, in conjunction with other research, as it offers hope for genetically improving blackwood stem form and reducing the costs of plantation management.

The use of nurse crops in blackwood plantations to help improve stem form, and to reduce management costs, has been of continuing research interest in Tasmania. However this study found that while nurse crops appear to improve stem form, this

comes with more complicated silvicultural management, compromised blackwood growth rates (Beadle *et al.* 2004), and now, as identified in this study, compromised wood quality (e.g. heartwood colour). Whether this negative nurse-crop effect is nurse-species dependant and due to competitive and/or allelopathic factors remains unknown. These findings suggest the use of nurse crops in blackwood plantations may be inadvisable, at least until further research in this area is undertaken.

Within the large, previously unassessed Oigles Road blackwood trial, the current study identified families of outstanding growth performance. These families may be used as the basis for initial early selection for thinning in this trial. However, a complete wood properties study of the Oigles Road trial should be considered a priority as it presents a significant opportunity to improve our understanding of genetic variation and control of wood properties in blackwood. The families identified as having outstanding growth performance and wood properties at Oigles Road could also be used as the basis of a trial cloning program to begin developing a collection of superior blackwood genetic material. This should include testing the clones in clonal trials across a range of sites, as well as offering the clones for immediate commercial deployment. The cloning strategy would allow immediate commercial gains to be realised from the Oigles Road trial, as it continues to be developed as a seed orchard.

The study found variation in important wood properties such as percentage heartwood, basic density, wood stiffness and heartwood colour. Significant environmental and genetic variation was found for many of these wood traits, together with some significant genetic by environmental interaction. There were few significant adverse genetic correlations and positive correlations included those

between stem diameter growth and wood properties. This holds the promise of achieving genetic gains from selecting and breeding for wood properties, while also selecting for improved growth and form.

Significant environmental variation and genetic by environmental interactions for some of these wood properties show that much still needs to be understood before genetic material can be matched to sites with a high degree of confidence. For example the environmental factors affecting blackwood basic density and heartwood colour remain elusive. Despite these continuing uncertainties, this study has made significant progress in our understanding of these variables. Blackwood selection and breeding for improved growth, form and wood properties can continue with improved understanding and confidence.

Selecting for improved growth and form is relatively straight forward, with simple available measures, and significant genetic effects evident in both early and later-age trials, to make these selections achievable and worthwhile in terms of genetic gain. However selecting for improved wood properties in blackwood is more complex, with potentially many traits to manage. Market preferences for blackwood at the level of individual wood properties are not known, and likely to vary between market sectors, and with changing consumer preferences. As a general rule higher basic density may be preferred in the veneer, furniture and joinery markets (Nolan *et al.* 2005), however the tonewood industry may prefer a wider range of basic densities. The variation in wood properties such as basic density, stiffness and heartwood colour, where market preferences may vary, should be managed through the development of product classifications and industry standards. This would allow market preferences in the separate sectors to be assessed, and form the basis for

selection and breeding objectives. More research is needed to identify preferences in the various blackwood market sectors for individual wood properties. A similar lack of publicly available market pricing information for the blackwood market sectors also limits the prioritising and allocation of resources in selection and breeding. Without this information the choice of key traits in the selection and breeding of blackwood remains largely a guessing game.

Of the 656 stem cores used in this study only one displayed figured grain in the form of fiddleback, which was insufficient to make any contribution in this area. Figured grain remains the "holy grail" for many blackwood researchers, growers and processors as it is in strong demand, and prices are accordingly high. Future blackwood genetic research should include figured grain as an important wood property to be assessed and studied. This will require improved methods for identifying this trait within standing trees. Research should include i) assessing the within-tree distribution and orientation of figured grain; ii) its frequency and distribution within the Tasmanian blackwood population; iii) the degree of genetic control, and iv) whether the trait can be captured by cloning.

Only two blackwood seed orchards are known to currently exist in Australia, both in the early stages of development. These are Farm Trees Pty Ltd, Bunyip, Vic. (www.farmtrees.com.au) and Oigles Road, Tas. (www.forestrytas.com.au). These two trials represent the best opportunity for continued research into the genetic variation and control of growth, form and wood properties currently available in Australia. The Tree Farms orchard was planted in 2002, contains 58 family seedlots including 69% of Tasmanian origin, is privately owned and is managed with the assistance of CSIRO. It was assessed for growth and form in 2006 although these

results have not been formally published (Chan and Lockwood 2007). The trial has now received two thinnings, resulting in only one of the original three trees per family plot remaining. The trial should now be suitable for wood property assessment. The publication of the 2006 growth and form results and a new measurement of these characteristics, together with a wood properties assessment, are research opportunities that would add significantly to current knowledge.

The Oigles Road trial, owned by Forestry Tasmania, has been affected by ongoing drought, and little ongoing management. Improved management may see this trial return to good growth, while a wood properties assessment of this trial represents a significant research opportunity, and should be done in conjunction with a first thinning. This would allow better estimates of genetic parameters for important wood traits to be calculated. Many Tasmanian family seedlots are common between the two seed orchards, presenting opportunities for better understanding the environmental controls, and genetic by environmental interaction on growth, form and wood properties. As mentioned above the families of outstanding growth and form at Oigles Road also represent immediate opportunities for clonal development of superior blackwood genetic material.

Both the Farm Trees and Oigles Road trials are dominated by genetic material of Tasmanian origin. This is largely due to the heritage of extensive seed collecting in Tasmania between 1988 and 1991. No comparable collections are known to have occurred in the mainland populations, and no continuing scientific collections are known. Genetic research on blackwood requires further sampling of native populations, with opportunities to recommence seed collections within both Tasmanian and mainland populations.

Wood colour research is a relatively new and minor field, reflecting the low level of research into appearance-grade species generally. Wood colour measurement was a key feature of this study, using stem cores to measure colour variation, and within-tree colour patterns. The extent of heartwood colour variation found in blackwood requires two outstanding issues for heartwood colour measurement to be addressed.

1. How best can overall vertical and radial within-tree mean heartwood colour and colour variation be measured; and can these colour traits be correlated with a non-destructive sampling method? Raymond and Bradley (2002) remains the only known study to have considered these sampling issues, using *Eucalyptus nitens*, and provides a useful starting point in any future research. Meaningful measures of between-tree colour variation can only be developed once the within-tree variation is better understood. Measures of within-tree heartwood colour variation should also be linked to the needs of industry, so that their preferences are reflected in selection and breeding programs.

2. How can a "mean" tree heartwood colour be derived? A mean tree heartwood colour value is needed in selection and breeding in order to understand and manage between-tree colour variation. These heartwood colour issues should be confined to a merchantable log length within the tree, for example the bottom six metres of stem, which is the prescribed pruned length (Nicholas and Brown 2002). This research could be usefully progressed using the existing blackwood trials in northern Tasmania used in this study.

Other research opportunities include understanding the relationship between colour measured on dressed radial surfaces such as those used in this study using stem cores, and dressed tangential surfaces. Blackwood is mostly back-sawn, resulting in the colour and pattern of the tangential surface being the dominant feature, and which is the key to understanding market preferences. If stem cores are to continue to be used in non-destructive wood sampling and colour measurement, then an understanding of the relationship between colour and patterns of radial and tangential surfaces are needed. Another project that could easily be done in conjunction with this is a study of the affect of various wood varnishes on blackwood heartwood colour. Harrison (1975a), using wood oil on a selection of blackwood samples, found irregular changes in colour from un-oiled to oiled heartwood. This suggests there is a range of extractives controlling heartwood colour which, when exposed to finishing chemicals such as oils, and perhaps varnishes, results in different chemical reactions. This is an important issue for the blackwood processing industry, but also would provide a better understanding of the relationship between heartwood extractives and colour. These projects could be based on blackwood offcuts from sawmills or furniture/cabinetmaker workshops, provided a wide range of heartwood colours could be obtained.

This study found significant age-age correlations in growth between early and later-age blackwood, indicating that early selection for growth provides for improved growth throughout the full rotation. Similar age-age correlations are also needed in wood properties.

Figure 8.1: Well managed blackwood plantation in New Zealand

Other research opportunities in wood properties include testing the tonal acoustic and other tonewood properties of blackwood over a wide range of basic densities. With global tonewood supplies continuing to tighten due to decreasing supply and increasing demand (Ellis *et al.* 2008), the requirement for sustainable plantation-based supplies is increasing (www.musicwood.org). Blackwood is one of the few traditional tonewoods that can help meet this demand (Figure 8.1). Blackwood has traditionally been used as back-and-side sets in steel-string guitars, but has also been used as soundboard material. These two applications require wood of different properties, and more research is needed to better match blackwood to meet both uses. This would allow blackwood breeders and growers to target these high-value markets more effectively.

As blackwood is primarily an appearance-grade timber species the resources potentially available for developing a breeding program are small compared with major structural/pulping species such as eucalypt and pine. However, blackwood does have advantages that continue to generate and maintain both domestic and international interest in the species. These include 1) a well established reputation as a premium timber, both in appearance and in ease of processing; 2) potentially rapid growth rates; 3) a wide ecological range and genetic variation that remains to be exploited in developing plantations from subtropical to temperate regions around the world; and 4) a small band of dedicated researchers who continue to rely on random *ad hoc* opportunities in finding and matching funding with available resources, of which this project is an example.

Tasmania has had, and will continue to play, a major role in blackwood research, if only because of its significant genetic resources. However, international interests are beginning to play an increasing role, particularly in New Zealand, China and Chile (Nicholas and Brown 2002; Zhang *et al.* 2004; Pinilla and Briones 2007). Cooperation and collaboration between these interests will be vital in maximising potential gains in the small world of blackwood research. However for selection, breeding and ongoing research, seed collections from native populations need to recommence, to rebuild genetic resources, and extend the range and size of first generation genetic material.

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Appendix 1: Family seedlots planted at Oigles Road blackwood progeny trial

Seed Zone	Family code	Name	Longitude (°E)	Latitude (°S)	Altitude (masl)	Date collected
1.Far North-west & west coast	1A	Kanunnah Big Tree	144.98	41.11	30	1/03/1988
	1B	Montagu West	144.88	40.98	40	26/02/1988
	1C	Plains Creek	145.03	40.92	30	9/03/1988
	1G	Argent Rd	145.39	41.76	170	8/03/1988
	1H	Kanunnah flutted	144.98	41.11	30	8/03/1988
	1J	Barcoo Rd	144.95	40.86	50	26/02/1988
	1K	Duck River	145.18	41.01	160	4/03/1988
	1L	Sumac 30	144.92	41.12	40	1/02/1989
	1M	Henty Rd	145.27	42.02	5	16/02/1989
	1N	Howards Rd	145.49	41.93	520	16/02/1989
	1P	Belmont Rd	145.54	41.38	500	28/02/1989
	1T	Badger River	145.35	42	140	19/03/1991
2. North west coast	2A	Sisters Creek	145.58	40.94	100	19/02/1989
	2C	Bunkers Hill	145.7	41.37	600	22/02/1989
	2D	Meunna	145.48	41.08	250	1/03/1989
	2E	Meunna	145.47	41.08	260	27/02/1991
	2F	Meunna	145.48	41.07	280	27/02/1991
	2G	Belmont Rd	145.54	41.39	480	7/03/1991
	2H	Belmont Rd	145.53	41.39	450	7/04/1991
	2I	Belmont Rd	145.56	41.39	600	21/03/1991
	2J	Bunkers Hill	145.69	41.37	610	21/03/1991
	2K	Bunkers Rd	145.68	41.36	580	26/03/1991
	2L	Amazon Rd	145.72	41.38	600	26/03/1991
	2M	Amazon Rd	145.71	41.38	620	26/03/1991
	2T	Lemonthyne	146.16	41.62	400	6/03/1991
	2U	Lemonthyne	146.16	41.62	400	6/03/1991
	2V	Stoodley	146.39	41.38	280	7/03/1991
	2W	Stoodley	146.39	41.38	280	7/03/1991
	2X	Beulah	146.39	41.48	300	15/03/1991
	2Y	Beulah	146.39	41.48	300	15/03/1991
3. West Tamar	3A	Warners Sugar Loaf	146.63	41.69	500	20/02/1989
	3B	Meander	146.58	41.7	560	20/02/1989
	3C	Mahoneys Creek	146.77	41.38	280	20/02/1989

Seed Zone	Family code	Name	Longitude (°E)	Latitude (°S)	Altitude (masl)	Date collected
4. East Tamar	3D	Brushy Rivulet	146.74	41.4	300	20/02/1989
	3E	Warners Sugar Loaf	146.64	41.67	440	26/02/1991
	3F	Warners Sugar Loaf	146.63	41.69	520	26/02/1991
	3G	Warners Sugar Loaf	146.63	41.69	500	26/02/1991
	3H	Meander	146.58	41.7	460	7/03/1991
	3I	Frankford	146.77	41.39	240	26/02/1991
	3K	Frankford	146.71	41.33	240	27/02/1991
	3L	Frankford	146.73	41.28	280	27/02/1991
	4B	Nook Valley	147.37	41.2	190	4/02/1988
	4C	Lisle	147.34	41.25	400	4/02/1988
	4D	Nabowla	147.35	41.21	200	6/03/1991
	4E	Nabowla	147.38	41.2	180	13/02/1991
	4F	Nabowla	147.37	41.19	160	13/02/1991
	4G	Nabowla	147.35	41.19	160	13/02/1991
	4H	Nabowla	147.36	41.2	110	13/02/1991
5. North-east	5F	Goulds Country	148.06	41.21	220	23/02/1988
	5I	Murdochs Rd	148.06	41.23	200	7/04/1989
	5J	Tebrakunna Rd	148.03	41.08	140	7/05/1989
	5K	Hogans Rd	148.05	41.39	200	9/06/1989
	5M	Terrys Hill	148.1	41.23	60	8/07/1989
	5N	Sweets Creek	148.17	41.41	350	8/08/1989
	5O	South Esk River	147.71	41.41	400	21/02/1991
	5P	Terrys Hill	148.1	41.23	200	21/02/1991
	5Q	Mt Michael	148.03	41.2	620	22/03/1991
	5S	Cuckoo Hill	147.64	41.23	600	27/03/1991
6. Central Plateau	6A	Lanes Tier	146.72	42.33	460	14/02/1989
	6C	Wayatinah	146.49	42.39	260	21/02/1991
	6D	Wayatinah	146.5	42.39	280	21/02/1991
	6F	Victoria Valley	146.72	42.33	460	21/02/1991
	6H	Lanes Tier	146.68	42.09	200	25/02/1991
7. Northern Midlands	7B	South Esk River	147.55	41.41	390	23/02/1988
8. South west	8A	Scotts Peak Rd	146.3	43.04	360	15/02/1989
	8D	Scotts Peak Rd	146.3	43.04	360	14/03/1991
	8E	Scotts Peak Rd	146.37	42.86	360	14/03/1992
	8F	Boyd Rd	146.29	42.83	360	14/03/1993

Seed Zone	Family code	Name	Longitude (°E)	Latitude (°S)	Altitude (masl)	Date collected
9. Derwent Valley	9A	Jacques Rd	146.7	42.81	440	13/02/1989
	9B	Salmon Ponds	146.99	42.76	40	13/02/1989
	9C	Dunrobin Rd	146.62	42.52	380	14/02/1989
	9D	Styx Rd	146.73	42.79	320	15/03/1991
	9F	Styx Rd	146.77	42.79	280	15/03/1991
	9G	Johns Tier	146.7	42.56	240	25/02/1991
10. East Coast	10A	Sandspit	147.84	42.71	200	1/02/1988
	10B	Murdunna	147.91	42.94	240	1/03/1988
	10C	Oatlands	147.49	42.31	400	9/03/1989
	10D	Oatlands	147.49	42.26	440	14/03/1991
	10F	Oatlands	147.64	42.27	400	26/02/1991
11. Southern Forests	11A	Creekton Rd	146.91	43.35	140	2/03/1988
	11B	Huon Rd	146.72	43.09	140	2/03/1988
	11C	Barn Back	146.79	43	300	10/02/1989
	11D	Sisters Bay	147.02	43.42	2	10/02/1989
	11E	Manuka Rd	146.72	43.09	100	19/02/1991
	11F	Arve Rd	146.78	43.12	160	19/02/1991
	11G	Arve Rd	146.79	43.15	160	19/02/1991
	11I	Weld Rd	146.81	43.03	160	19/02/1991
	11J	Griggs Rd	146.81	43.02	160	20/02/1991
	11K	Griggs Rd	146.81	43.02	200	20/02/1991
	11L	Griggs Rd	146.8	43.03	220	20/02/1991
	11M	Weld Rd	146.81	43.04	100	20/02/1991
	11N	Denison Rd	146.76	42.97	160	20/02/1991
	11O	Esperance	146.95	43.33	60	20/02/1991
	11P	Esperance	146.94	43.33	80	20/02/1991
	11Q	Esperance	146.93	43.31	80	20/02/1991
	11R	Esperance	146.93	43.31	80	20/02/1991
	11S	Esperance	146.93	43.31	90	20/02/1991
12. King Island	12A	King Island	144.09	39.9	80	1/02/1988
	12B	King Island	143.97	40.05	95	21/02/1991
	12C	King Island	143.96	39.99	100	21/02/1991
	12D	King Island	143.96	39.94	90	21/02/1991
	12E	King Island	143.97	39.88	40	21/02/1991